

L. van der Pijl

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Principles of

# Dispersal in Higher Plants

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Third Revised and Expanded Edition



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# Principles of Dispersal in Higher Plants

by *W. G. S. J. van der Meulen*





L. van der Pijl

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Third Revised and Expanded Edition

With 30 Figures

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The cover motif shows water burrs with the double function of transport (via attachment to animals) and of establishment (anchoring to the substrate).

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## Preface to the Third Edition

The second edition was a hasty one, prepared in hospital only with the help of amendations on typed slips. The present revision has been more thorough, so that contents and references were almost doubled compared to the first edition.

Even more emphasis has been laid on ecology (including synecology), evolution and establishment after transport. The temptation was great to present these points under a new title, which would also have avoided being quoted with data (as being the ultimate wisdom) from the 1968 edition sitting in the local library. The publisher, though very liberal in satisfying needs, is, however, at the same time very moral and conscientious in his marketing methods, which means maintaining the original title. This though he, too, profits from selling one's "principles".

I regret the time did not allow inclusion of the results of the Symposium on Dispersal and Distribution, Hamburg, 10–12 June 1981.

It seems polite to react to criticisms by some reviewers:

A. On the loss of readability by the numerous cross-references: The very compressed text of a textbook should be studied, not just read.

An ecosystem is a web with many internal connections – and so is an ecological book, where aspects from different chapters have to be interconnected for coherence without repetition in each.

B. On complaints that an author's index and a glossary are lacking: Such an index would only be necessary in a more historically orientated review – and a glossary for terms is superfluous as the subject – index refers to definitions special to our field.

The Hague, Spring 1982

L. VAN DER PIJL

## Preface to the First Edition

The work offered here is a companion volume to the work by K. FAEGRI and L. VAN DER PIJL, *Principles of Pollination Ecology*, which deals with the preceding phase of reproduction in plants.

In the present work too, the emphasis is on principles and ecology. It is neither an enumeration of mechanisms, nor a compilation of cases. RIDLEY's monumental work *The Dispersal of Plants Throughout the World* comprises 700 large pages of small print, and research has proceeded since then. Though this work is more than just a compilation and contains much insight and thoughts on principles in addition to reviews, its completeness hinders its use as a textbook. As a reference work, it is unsurpassed and the writer made frequent use of it.

The writer paid special attention to functional backgrounds for the use of taxonomists working with "characters" and to biosystematics at the macro level.

He is indebted to Dr. P. MÜLLER-SCHNEIDER (Chur, Switzerland) for the permission to translate parts of his *Verbreitungsbiologie der Blütenpflanzen* – of which permission a modest use has been made. Thanks are also due to the Director of the Rijksherbarium at Leyden, and to its librarian for the use of the library.

Mr. F. J. NATAN was so kind as to take a number of photographs at the author's request.

Prof. Dr. H. F. LINSKENS stimulated the work actively and made completion possible with the collaboration of the members of his staff at Nijmegen University, amongst whom Miss I. DE ROOS should be thanked especially.

Prof. Dr. B. J. D. MEEUSE (Seattle) was of great service, criticizing the manuscript.

The Hague, Summer 1968

L. VAN DER PIJL



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# I. Introduction

## A. The Place of Dispersal in the Chain of Life

Microbiologists' concepts are seldom concerned with dispersal and areas of distribution. One of their rules, sometimes indicated as "Beijerinck's law", states: everything is everywhere, but the milieu (environment) selects. In microbiological terms, this means that a special substrate can demonstrate the presence, and promote the development, of certain microbes specialized for that substrate. Such lower organisms are evidently so easily spread that they are in principle not limited by the dispersal factor. Some fungi and mosses requiring special substrates (e.g. dung) have advanced beyond this point, developing devices for directed transport of spores to preferred substrates; and in the higher plants, in which spores have lost their general function of dispersal, the same purpose is served by the microspores which are brought to the stigma. This directed transport of microspores is dealt with in pollination ecology. In higher plants, colonizing dispersal is a factor limiting distribution more severely.

In this book, we have to study the ways and means which the higher plants employ to reach, with their newly developed dispersal organs, sites where a new generation can be established. More specifically, this involves the methods used to keep their descendants separated in space and to provide each with its own site, where it can compete with other plants; it also concerns the methods employed to defend the future of the species by exploring new territories, particularly following climatic fluctuations, or conversely to maintain a foothold on a favourable site.

Another feature of spores, the power to withstand and survive unfavourable conditions over a long timespan, is also evident in the reproductive organs of higher plants. The products of these organs, such as seeds, may combine the advantages of dormancy with those of genetic variation, in contrast to vegetative resting organs, which merely continue the life of the individual without hope for the future of the species in a changing environment.

In the present study, we shall have the opportunity to emphasize two different aspects, viz. actual dispersal as studied in the field, and the structural basis needed to attain this dispersal; both will be considered in an ecological context. All too often, the second aspect has predominated so strongly in works on dispersal that they remain examples of herbarium ecology, or worse, writing-desk ecology. Nevertheless, the structural aspect cannot be dismissed as the starting point, the more so since a mere enumeration of findings in certain sites (as by Heintze, 1932) produces an unmanageable chaos.

We must be aware of the fact that dispersal is but one link in the continuity of life on earth, which is perpetual colonization. It starts with presentation of the dispersal units (including dehiscence and detachment), if possible at the right time and place, as a preparation for dispersal. This preparation also makes travel possible by providing physiological and structural protective devices. After travel comes settlement, not always by mere deposition, and germination. Only then does the question arise of a substrate suitable for establishment. We shall discuss dehiscence and its mechanisms only incidentally, viz. when they are connected with special ecological factors. The important contribution of Fahn and Werker (in Kozłowski, 1972) pays attention to anatomical details. So do those by Straka (1962) and v. Guttenberg (1971). Though presented under "dispersal", the structures described are mostly just presentation devices.

Any of these parts of the whole phenomenon can be the bottleneck, and in a plant community any of them can be dominant. As the various aspects of the overall process are also reflected in the structure of dispersal units (outside mere dispersal function), there is all the more reason to study them. Sometimes anti-dispersal mechanisms are important for homeostasis.

We shall see in detail in Chapters VI and VII, and elsewhere, how unsound it is, biologically speaking, to limit our attention to mere transport. All aspects intermingle and may change in importance during succession and evolution, so that in the dispersal organs we shall find traits relating to other spheres of life. We shall try to keep these various features apart for heuristic reasons.

The general effects of seed dispersal, discussed before, should be augmented by newer aspects. Next to pollen transport, seed dispersal is the most important single factor promoting the gene flow in populations. Grant (1958, 1980), for instance, has pointed to the effect of good dispersal on variability in populations of *Juniperus* in contrast to the situation in *Cupressus* species. Ehrlich and Raven (1969) neglected this factor entirely when stating that pollen rarely has a long-range transport and that gene flow is therefore less important than is generally thought. Janzen (1970) emphasized for tropical seeds the importance of distantiation from breeding places of seed-predating insects, a special aspect of the separation from the mother plants mentioned before, which provides escape from local antagonistic influences (see pp. 47, 102).

Whereas animals can actively select a habitat, plants are generally passive, dependent on chance and a vector. In cases of high-quality dispersal we find some dirigism to a favourable habitat. This may include promotion of germinability.

I shall often avoid the trodden path of temperate ecology and refer to tropical phenomena, in the first place to be more universal, but also to be more fundamental, since the impoverished temperate conditions, which prevail for certain herbs and pioneer plants in temperate regions, are not truly representative.

It is also necessary provisionally to point out here that in seed plants the dispersal organs arise ontogenetically out of so-called sexual organs, the flowers, and therefore still manifest properties of the latter (see p.17). When coining terms, it will prove important to reckon with these remnant conditions.



## B. Limitations and Objections

Just as was the case with pollination ecology (cf. Faegri and van der Pijl, 1979), dispersal ecology fell into discredit in the twentieth century for being partly the writing-desk ecology mentioned above. Many nineteenth century authors saw selective advantage in, and ascribed a dispersal function to, each and every detail of fruits. Some explained the distribution of plants on this basis alone. I must, however, point out that the first composer of a systematic account of dispersal (Hildebrand, 1873) already warned against such simplification. So did Kerner in his (often reprinted) *Pflanzenleben* (1891).

Just as in floral ecology, the resistance of the time had many roots. One of the objections was based on the anti-Darwinian attitude of some morphologists and new physiologists, who preferred so-called antiteleological explanations from their own fields. Goebel was of the opinion that the morpho-physiological pluriformity, as just given, had obtained a function only secondarily, by "utilization". In the field of flower structure his work *Die Entfaltungsbewegungen* (1924) is full of antiteleological "proofs", nowadays mostly acknowledged as beside the point since the directed functional development has in many cases become clear. He stated that many "adaptations" in fruits should be "killed", apparently as they did not lend themselves to be explained away as a mere repetition of unfolding movements. Other anti-Darwinists, like the Lamarckistic school of Clements (1950), emphasized certain (misunderstood) cases to deny their survival value. For example, they ascribed the composite pappus to "correlation" in most cases without functional value. The reader may find in the index to this book many connections between deviating pappus and special ways of dispersal.

Obviously influenced by his work on sea dispersal, Guppy (1906) was a strong advocate of just utilization as a background. He stated (compiled from his pp. 100–102): "Nature has never concerned herself directly with providing means of dispersal; the sticky layer on some seeds exists for secretion; the dispersing agencies take advantage of certain characters developed for other reasons and thus representing results of history; the principles of evolution and adaptation rule the world except in dispersal."

I wish to remark that this concept may be valid in many cases. We speak of "pre-adaptation" when a structure or chemism can assume a new function in a new combination or under new circumstances. Such a concept, however, does not always represent the whole truth: the combination of various "usable characters", which we shall often meet, points to development in a certain direction. Coconuts, for instance, are not just accidentally sea-dispersed, as we shall see.

The other ideological basis for disbelief in adaptation was a somewhat supranatural belief in immaterial forces and "Gestaltphilosophie" behind form. This typological approach, often applied to flowers, did not find a fertile soil in dispersal biology.

An attack on dispersal functions and adaptation was made from quite a different angle, namely by considering the fruit solely as an organ of germination, this probably also for ideological reasons. Gindel (1960) denied its function in

dispersal, considering its attractiveness as accidental. The juicy fruit is, according to him, an organ which ensures continuing life at germination, so that it is imperative that it remain intact. Dead and infected fruits and loose seeds give, according to his experiments, poor germination. Dry fruits, obviously, were not taken into account. Mayer and Poljakoff-Mayber (1963) have already criticized this queer concept.

Ridley (1930) and others have given us an abundance of cases of correlation between area extension and the presence or absence of dispersal mechanisms. Many plant geographers, however, starting with de Candolle in his *Geographia Botanica* of 1855, have apparently been so impressed by the incongruity between area extension and dispersal mechanisms in other cases that they neglect dispersal entirely, even when discussing the migration of floras. See, however, the case of *Dolichandrone* on p.76.

Illustrative are the writings of Croizat, who discusses distribution only, calling it, however, dispersal. Migration implies dispersal and this requires some mechanism. In one of his many publications (1968) he stated that means of dispersal should be excluded from scientific biogeography. He had argued before that species with apparently excellent means (like some pappose *Solidago* spp. in North America) are very limited in distribution, so that dispersal mechanisms are redundant. See, however, p. 186.

We cannot discuss here the supposed migration routes suggested by plant geographers, and mainly based on comparative counts of species and genera. They often draw pathways on recent maps, neglecting the geographic situation at the times concerned. We shall also be reluctant to accept uncritically "land bridges" and continental drift as full explanations. Of necessity, however, some consideration of ancient, now wide disjunctions connected with drift, independent of dispersal, will have to follow, especially in the chapter on island floras. We shall remain silent on "age and area". The existence of development centers of taxonomic groups with far-flung outposts implies dispersal. Outposts are not done away with by always interpreting them as relicts. The truth in the thesis that plant species move only in associations has yet to be confirmed.

Indeed, dispersal and its attendant phenomena require much more study, although what has been achieved up to now deserves a textbook, not merely the "jeremiad" of Webb (in Hawkes, 1966) that what statements there are, are cloaks for ignorance. History, including changes in the global crust, is not repeatable, but its forces can be adstruced by present-day processes.

We shall not discuss lower plants. Their dispersal is not always so simple and generalized as we stated in our opening sentence. The fungi, especially, have sometimes reached high precision and contact with all kinds of vectors outside their primeval water and the succeeding wind. These endless refinements have been reviewed by Ingold, most recently in 1971.

## C. History and General Literature

The field of study was for a long time dominated by Scandinavians. Linnaeus and some pupils were among the first to perform experiments, even feeding seeds

to animals to study the results for the seeds. Holmberger published in 1785 a *Theory on the Dispersal of Plants over the World* in which he recognised the seven main dispersal classes. The linnean concept of origin *ex unico loco* played a role herein. Much later, some Germans (Sprengel, Kerner) as well as Delpino became interested, as did Darwin, who even performed experiments on buoyancy and on germination of seeds transported on the feet of waterfowl. Hildebrand produced the first modern, comprehensive review. This was, curiously, in the same year (1873) that Hermann Müller produced his fundamental work on floral ecology, and about the same time that Delpino published his important work on the latter topic.

Kerner (von Marilaun) published his experiments on various topics in 1863 and inserted them into a chapter of his large popular work *Pflanzenleben* (1891), translated as *Natural History of Plants* (1896). The work of Delpino (1870–1905) in carpobiology is so imbedded in existing foundations that it is now forgotten. The Scandinavian Dammer (1892) coined many terms and produced (for Polygonaceae) the first paper on dispersal mechanisms within a family. Sernander (1906, 1927) inspired a number of pupils. His collection of carpologia is still kept in Uppsala.

Heintze (1932) started a handbook of which only two instalments appeared. Although he gives useful reviews of the history of terms, the book is brain-wrecking by its confused nature and inadequate references. Ridley consistently misspells his name as Heinitz.

Of the later books, also written in German, mention should be made of Ulbrich (1928) and Müller (1955, reprinted 1977). The first is rather general and well documented on mechanisms, the second more limited in pages and in scope, very European, though very readable and with a broad background. In English we possess two general, popular American booklets. The first, by Beal (1898), contains original contributions on a schoolbook level, the second (Matheny, 1931) could not be consulted, but is said to have the same character.

Some books by Guppy (1906, 1912, 1917) of a mixed nature contain important new observations on sea dispersal. The dispersal bible by Ridley (1930) is a monument indispensable to any writer on the subject, including the present author, as a reference book. In our book we will, for the sake of brevity, often make do with a reference to Ridley, also for the older literature.

The French have to make do with a long series of journal papers by Molinier and Müller (1938), the latter the same as Müller-Schneider, often cited.

Russian botanists, during the last decades, have shown much interest in the field, but mainly in fruit systems, as far as can be judged. The book by Levina (1957) apparently summarizes data for national use.

Very old literature from the 18th century up to 1905 is collected in Campagna (1905); that of the period 1873–1890 very thoroughly in MacLeod (1904). I shall concentrate here on literature that appeared after Ridley, or was not cited by him.

## II. General Terminology

In the first place, we must consider the name of the phenomenon under discussion. "Dispersal" was indicated expressly for English use by Praeger (1923) and supported by Ridley. They defined it as the active (dynamic) process of transportation, differentiating it from the result it leads to: the passive (static) state of distribution. Unfortunately, this scientific distinction seems insufficiently reflected in colloquial English. Jackson's glossary gives the two terms as synonyms. Henderson's *Dictionary of Biological Terms* does better. Scandinavians differentiate between "spredning" and "utbredelse", but Dutch botanists maintain confusion as illustrated below for English. I found a line: "on the influence of 'verspreiding' on present 'verspreidingspatroon'". In other languages, too, common usage makes no sharp distinction between the comparable words, so that foreign terms came into scientific use. Though I often use it, I shall not promote the use of the term "dissemination" in English for reasons to be explained below, although the other terms may cause confusion. A study entitled *Ancient Dispersals* proved to deal with distribution, and a paper called *Distribution by Means of Bats* concerned dispersal. The (translated) book of Takhtajan *Flowering Plants – Origin and Dispersal* is practically silent on dispersal, but treats distribution well.

Some papers use the term "dispersion", which is simply incorrect, having an established other meaning.

The term "dissemination" is often used for a part of the overall phenomenon, more or less what we distinguish as "presentation", namely, the act of discharge or liberation of the seeds. Some authors (Falinski, 1971) wish to reserve the term "dissemination" for the phase after the transport. Stopp (1958 b) preferred it to the confusing German terms for dispersal and distribution. (The proposal of Christiansen, 1954, to use respectively "Ausbreitung und Verbreitung" is alas rarely followed.) So do the French and the Italians. Stopp gives it a wider scope than just "dispersal", including later processes. I can object to this term, and the widening, only because the word "dissemination" refers to seeds, not to spores and vegetative diaspores. Pollination is spore dispersal, not spore dissemination. One would also prefer a more general term applicable to zoology. The term "propagation" also meets with objections.

"Migration" is wrong in this context, as it denotes in zoology the mass displacement of a mobile existing population. For long-term phenomena involving shifting vegetations the use of this term may be continued in preference to "expansion".

Next come terms for the branch of science embracing our field, a question avoided in the title of this booklet. We shall see that "chorology" is the correct



term, but unfortunately it seems to be pre-empted in current botany. "Dispersal ecology" might form a parallel to "pollination ecology". Ulbrich (1928) used as a subtitle "carpobiology", which is at the same time too wide and too narrow.

We have to move on to the smaller categories in our field, discussing the separate links of the overall process. Dammer (1892) used the suffix "-chory" (*chorein* = to wander) behind the name of the agent for classes of diaspores transported by this agent. This has been generally accepted and later authors (such as Nordhagen) used the term "chorology" for the whole field of knowledge. Since Rübel (1920), however, the term has been usurped by plant geographers for the subject of plant distribution, probably interpreting "-chory" as derived from "place". Barkmann (1958) used "chorology" broadly, subdividing it into four categories, according to static, dynamic, causal and historical aspects respectively, and placing dispersal in the second category.

The suffix "-phily" (= friend) will here, as usual, be combined with the same agents to indicate the mode of transport of spores, especially microspores and their successors, the pollen grains. This transport of haploid dispersal units thus concerns pollination phenomena, originating in Pteridosperms.

The neutral suffix "-phily" emphasizes the specific dispersal to a "friendly" place, ultimately the stigma. Important aspects are its asexual character (despite Linnaeus) and the morphological continuity of this spore dispersal in lower and higher plants (cf. Faegri and van der Pijl, 1979). A fungus, a moss and a flower having their spores transported by wind may all be called anemophilous.

Some terminological difficulty arises when isospores of lower plants are considered as merely serving the purpose of dispersal and falling under the "-chory" category. In these plants "-chory" and "-phily" are not yet differentiated and may both be used, for instance "autochory" for a fungus or fern shooting its spores away. The undirected dispersal element stands here in the foreground, even though one might point out that it is just the first step in the presentation to wind or animals, and also that the spore dispersal is but the first step towards establishment of a new diplont. In old publications "-phily" was used for dispersal categories, too; also in Dansereau and Lems (1957).

The suffix "-gamy" (*gamein* = to marry) has to be reserved for purely sexual processes, such as the transport of and the differentiation between gametes. From algae up to some Gymnosperms we find their transport taking place in water: hydrogamy. Later on, siphonogamy, porogamy, etc. arose. I must again admit a weakness in the lower regions of the plant kingdom. In algae, the transport of spores and that of gametes is not yet clearly differentiated in character, and consequently not in terminology. The French preference for "-gamy" in terms relating to flower pollination is perhaps understandable, but should be condemned as a Linnean prematurity to the real sexuality. Zoidiogamy refers to swimming spermatozoids, not to pollen transport by animals, as is often said.

The suffix "-spory" points to some peculiarity of the diaspores.

Now that we have touched on national feelings it becomes necessary to proceed. In classification generally two different aspects can be emphasized, resulting in two approaches. One is the delimitation of classes to obtain a clearcut sys-

tem with sharp boundaries. The other is to find common characteristics in a group, pointing to common relations to a certain factor. An ideal system uses dividing walls to separate, as well as nuclei to concentrate and to include – as in an organism. In German handbooks, the dividing walls are often stressed. In contrast, the Englishman Ridley had an aversion to classification and its terminology, claiming that terms are not essential and abandoning “dissemination” for the more vague term of “dispersal”. Although classifying his cases in orderly fashion, he denied that a natural category deserves a special term. In actual fact, the coining of terms makes the subject matter easier to handle, especially by resorting to the use of adjectives. For example, one can time and time again speak about certain plants as having characteristics in their seeds or fruits which cause these to be regularly transported by ants. It is, however, simpler to say that such plants are myrmecochorous (a term especially despised by Ridley).

One might expect here definitions of the different organs of dispersal. However, I shall refrain from such definitions, as a thorough analysis of what constitutes an ovule, a seed, or a fruit in the different groups of seed plants, and an inquiry as to the origin of their constituent parts, would lead to premature and out-of-place phylogenetical and morphological speculations. For the simple descriptive enumeration of fruit forms, the reader may refer to morphological textbooks. We shall preferably restrict ourselves to functions and provisionally to classical ideas on carpels and ovaries, even though this field is in constant flux (Meeuse, 1966, and later papers).

In general, it seems superfluous to create terms for the units adapted to different agents of dispersal; in the following chapters, where we shall investigate how they function and how their structure changes over time, the morphological terminology (which already has an ecological background) is usually sufficient. Terms for each functional modification in a morphological unit would result in chaos.

Dansereau and Lems (1957) felt a need for some semifunctional system and for semifunctional names for diaspores when they constructed the dispersal spectra used for quickly characterizing communities. They created classes of diaspores based on apparent structure for dispersal, regardless of whether these would turn out to fulfill their “obvious” functions or not. Although this is not yet the occasion to criticize their system, I must point out that classes based on just one or two visible characteristics are far too simple for use in general ecology. The creation of such simple classes neglects colour, taste, smell and the real function (as we shall see on pp. 83 and 173), and does not reckon with arils or such important details as atelechory. The rather negatively defined group of the “sclerochores” of Dansereau and Lems contains hydrochorous nutlets, myrmecochorous diaspores, mimetic diaspores, beans, beech-nuts, etc. For “barochores” see p.89. The “ballochores” (diaspores forcibly ejected from the parent plant) are in reality very heterogeneous, as we shall demonstrate, and the characteristic structures are rarely situated on the diaspores, being usually present on organs of the mother plant (see also p.84).

A general nomenclatural objection, related to the last remark, is that terms pertaining to properties of diaspores (not directly to agents) should end with the suffix “-spory”. Clements used it in his parallel terms for comparable use as early as 1905. I fear that the terms discussed may cause confusion with terms ending in “-chory”, which already exist in general dispersal ecology, and that there is considerable overlap. Further terms follow in our respective chapters. Readers overwhelmed by the multitude of names may perhaps be appeased when learning that inclusion of those used in the fruit systems (to be discussed on p.16) would have brought in several hundred more.

### III. The Units of Dispersal

Ever since Sernander (1927), the plant part to be spread has been indicated, independently of its morphological value, as "diaspore" (from *diaspeiro* = I broadcast). Sometimes we find the terms "propagule", "germule", "migrule", "chore" or "disseminule". Sernander also gave a simple system, repeated here with some modifications. Its inadequacies will appear in the chapter on evolution. The system does not, of course, depend on function and agents, and is thus of little importance to us here.

- A. Spores (in lower plants).
- B. Haplonts (see Chapter VIII).
- C. New diplonts with envelopes (usually indicated as generative units).
  - 1. Nude embryo.
  - 2. Nude seed by itself (primary and secondary gymnospermous plants, see p. 135).
  - 3. Seeds liberated from dehiscent fruits (with or without arilloid).
  - 4. Fruits. From one ovary (simple fruits) or from many ovaries in one flower (aggregate fruits).
  - 5. Spurious (false) fruits or pseudocarps. From ovary plus other parts.
  - 6. Multiple or collective fruits, from inflorescences (syncarps).
  - 7. Seed contained in whole plant or part thereof (e.g. tumbleweeds).
- D. Vegetative parts of the old diplont.

It seems necessary to discuss the types C-1 and D separately here and now.

The nude embryo seems, at first sight, theoretically important as a transition from types A and B. Scattering of embryos is said to occur in *Selaginella* and other higher Pteridophytes. However, it may be an incidental regressive adaptation to water in the habitat. Indeed, this is the situation in the aquatic Angiosperms to be discussed under hydrochory and vivipary (see Ridley p. 187), and also in seeds dispersed by water animals (? *Inga*). For *Oxalis* see p. 116. In other cases (Loranthaceae) where the situation is not quite comparable, we find a testa-less seed with endosperm. This facilitates fast germination on branches, but on the other hand it may be seen as just a consequence of the reduction of floral organs in these parasites. In some Acanthaceae the outer layers of the nude endosperm take over functions of the seed coat (Bathnaga and Johri in Kozlowski, 1972). A connection with a special habitat is not clear. See p.78.

## Vegetative Parts in Dispersal and False Vivipary

The role of vegetative parts will not come up in later chapters, so we must deal with it here in a definitive manner. For descriptive compilations see Möbius (1940) and Weber (1967).

We leave aside persistent subterranean parts that function only as a reserve for the individual plant and as survival organs for geophytes, though rhizomes and stolons may produce new individuals nearby, sometimes promoted by pronounced fragmentation by means of abscission of rhizomes (*Rumex*, *Plantago* spp.). They contribute to mass expansion of individuals arrived as seeds; they may provide definite settlement, even when sexual unbalance in a new habitat hinders seed formation. The floating away of torn-off rhizomes, as it occurs in many water and beach plants, including grasses, can become the main, or sole, mode of dispersal. Such was the case with *Acorus calamus*, the sweet flag – which at an early date was introduced into Europe by man and is there sterile, due to triploidy.

Human dispersal of rhizome fragments explains the occurrence of some special clones over a wide region, (e.g. of male *Petasites* only).

In aquatic plants, fragmentation of stems and stolons can easily take over the dispersal function from seeds, as was the case in *Elodea canadensis* when introduced into Europe (one sex only introduced or maintained, and thus sterile) and in *Lemna* spp., where flowering is (? consequently) rare. In the tropics, well-known cases are *Pistia stratiotes* and *Eichhornia* (*Pontederia*) *crassipes* (the latter also sterile after introduction). Mass transport of whole plants is frequent in the “sudd” (floating vegetation) of tropical regions.

In epiphytic plants the transport of branches has been observed for *Tillandsia usneoides* when birds used them as nest material (Kuhlmann and Kühn, 1947). *Lemna* is vegetatively transported on the feet of waterbirds. Some cacti (jumping cholla) use epizoochorous fragments.

The distinction between vegetative parts serving for reserve and rest and those for dispersal is, of course, vague. Droppers or bulblets of bulbiferous plants can be established again at a distance after disturbance of the soil, for instance one caused by ploughing (Galil, 1965, for *Allium ampeloprasum*). Such dispersal function is differently expressed in tubers of some *Cyperus* spp., as *C. bulbosa* and *C. isochadus*. For those of *Oxalis* see p.13.

Dispersal of vegetative parts can overcome many of the hazards of seedlings. The simplest bulbils are perhaps those from some Greenland *Cerastium* and *Stellaria* spp., where the not-transformed apices of the stems fall off and root.

Special vegetative dispersal organs are not known from woody plants, on the contrary, they are frequent (and easily detached with a pure dispersal function) in annuals and especially in herbaceous perennials. The rule that an apomict can use wide seed dispersal and that vegetative reproduction lacks this possibility is not always valid. Some are seed-like and possess dormancy. They are commonly indicated as bulbils, even though their morphology may be heterogeneous; often they represent swollen roots with an adjoining axillary bud, as in *Ranunculus fi-*



*caria* (some tetraploid forms), where they are dispersed by rain wash. The "bulbils" on the tip of the leaves of the orchid *Malaxis paludosa* are so small and undifferentiated that they have been indicated as foliar embryos.

Some bulbils are thrown by ballistic mechanisms (*Dentaria* or *Cardamine bulbifera*).

The genus *Dioscorea* produces tuberlike bulbils, dispersed also by water, even overseas. In Indonesia the genus *Globba* has some forest species which rarely fruit, instead producing bulbils from axillary buds in the inflorescence.

When such detached bulbils have the character of young plants that sprout immediately, the term "vivipary" is often applied. This started with Linnaeus, because he thought that in such grasses seeds were involved, whereas their bulbils are shoots from the lemmas, just a kind of proliferation. Even Ulbrich and Müller consider this as true vivipary in contrast to the early sprouting of seeds on the mother plants, to be described later in a special chapter (p. 117). I do not agree, considering it at the most as "false vivipary" for the following reasons. The limit between early and late sprouting bulbils is vague; all easily sprouting vegetative parts such as subterranean stolons and bulblets would also fall under the term, and thereby the possibility of comparison with viviparous animals (bearing sexual products) would be lost. Many plants with inflorescences bending down and producing plantlets on the soil would have to be described as viviparous; e.g. the *Chlorophytum* cultivated as a house plant, or tropical species of *Marica* and *Limnorcharis*. The so-called viviparous ferns have no "-pary". The term "gemmaferous" (usually reserved for the process in the haploid phase) might be used. Fast and secure colonization seems important for ferns to skip the delicate haploid phase in dry habitats.

Well-known cases of bulbil production are temperate *Allium* species, *Polygonum viviparum*, *Poa alpina* and other grasses. In *Poa* we find dispersal by wind, in *Polygonum* by birds that treat the bulbils as seeds (they are often found in the gizzards of grouse, *Lagopus*, which regurgitate some of them undamaged). In tropical regions, *Bryophyllum* bears bulbils on leaves and *Agave* in the inflorescences. The last two cases are somewhat comparable with true vivipary, as the effect is not just dispersal but fast establishment in a rainy period, as discussed on p. 119.

As a sequence to dormant apices or offsets (*Ceratophyllum*, *Hydrilla*, *Stratiotes*) some water plants produce special, hardy, dormant buds sinking in the mud against wintertime for survival; these are indicated as gemmae, hibernacula, winter buds, or turions, and may assist dispersal by fragmentation. Species of *Utricularia*, *Myriophyllum*, *Potamogeton* show this, in the latter accompanied by low seed production (Muenscher, 1936).

Special bulbil-like buds on leaves occur in tropical *Nymphaea micrantha*. They sprout much faster than seeds. For marine *Cymodocea* see p. 73.

Typical dispersal bulbils are produced by some tropical Araceae. In *Gonanthus pumilus* these bulbils have long hairs (anemochory), in *Remusatia vivipara* they are provided with hooks like a burr (see Fig. 1). In the latter case, the

**Fig. 1.** *Remusatia vivipara*. Stalk with bulbils



flowers have sterile pollen, at least in Java. The plant was found in isolated, oceanic Christmas Island, far south of Java. In Africa it seems flowerless.

In many cases (also in *Ranunculus ficaria*), a correlation exists between sterility and the presence of aerial vegetative propagules. The latter cannot be dismissed as just an incidentally discovered way out of the danger of the former. There may exist a direct physiological relation (? hormonal) between the two, with each as possibly primary – as seen in species of *Allium*, where removal of bulbils in the inflorescence promotes the ripening of fruits. In the Irish potato the prevention of tuber development has the same effect on sexual organs. The reverse influence is more evident in *Lilium bulbiferum*, where bulbils arise in case of nonpollination of the flowers.

The genus *Oxalis* often produces small bulbs underground. In *O. cernua* these detach easily as hardy, seedlike bulbils. In the Mediterranean region this allopolyploid hybrid is sterile; moreover, only the short-styled form has been introduced, so that the bulbs must be responsible for its wide distribution there

outside gardens. This seemed at first enigmatic since in Israel the plant is found even in rock fissures high above ground level. Birds, however, eat and disperse them (Ridley, 1930 p. 462). Galil (1967) described dispersal of the bulblets by mole-rats (*Spalax*), blind, burrowing rodents that construct underground "granaries" with food reserves. Ridley relates (p. 382) that squirrels store bulbs of *Liliaceae*. Those of some *Allium* spp. in sub-deserts have hard tunics and can be blown over the surface (eolic drift). Thus all classes of dispersing agents have now been found to be represented in bulbils, though special attractant parts for endo-zoochory have not been found.

We have discussed the physiology of bulbils, which is important for ecology. The physiological influence of temperature and day-length will not be taken up here, but often a clear regulative relation has been found with some extreme condition that antagonizes normal sexual propagation. There is also some concurrence with apomixis and polyploidy. In addition to (sometimes diploid) *Poa alpina* some grasses of the genus *Deschampsia* show in arctic regions a tendency to bulbil formation, increasing with the chromosome number (Flovik, 1938).

We find one aspect of true seeds lacking in these cases, viz. the transport of a new genetic combination after recombination. This aspect is also absent in seeds originated after apogamy, but we shall not discriminate against them in the following sections. It remains, moreover, questionable whether even nucellar embryony is purely asexual. Internal processes, including semimeiotic nuclear processes, can provide genetic rearrangement and physiological restitution (perhaps new messenger RNA) in the cell. The term "uniparental reproduction" seems more suitable here, but it would also include real vegetative reproduction and selfing, so that "parasexual" is to be preferred. Alas, this term has recently come into use for fusion of protoplasts, with sometimes also ensuing genetic recombination.

## IV. The Relation Between Flowers, Seeds and Fruits

### A. Seed and Fruit

Since the rise of Pteridosperms, the seed has become the normal organ of generative, recombinative dispersal. Why then the fruit? In Chapter VIII we shall see in detail that the fruit is in principle an interpolation, the continuation of a new organ of the flower, the ovary. This persisted after flowering and, after a phase where it was more of a nuisance, it usually became an auxiliary organ of dispersal which supplanted the seed as such. Morphologically the difference between the two seems clear: the one arises from an ovule and the other from an ovary. Difficulties arise when we consider whether all ovaries are comparable or not, and whether perhaps some ovaries are homologous with seeds. As long as this does not involve ecology, we might leave these questions to morphologists, but this attitude becomes untenable when we realize that pure morphology is an abstraction, that morphology is perhaps the crystallized or fossilized ecology of former eras.

As long as we considered present temperate conditions as normal, basic and eternal, we had no trouble with the classical concepts mentioned, nor with those of fruit and seed. The seed then was assumed to be essentially small, hard and dormant, finally liberated from the fruit. We shall have to discard such assumptions.

Such concepts but rarely ascribe an independent role in dispersal to the seed, although admitting such a role for small anemochorous winged or plumed seeds. In archaic and many tropical seed plants the seed still plays the more active role described in Chapter VIII, with the intervening fruit secondarily repeating the functions and structures.

In our description of the ecological classes we can, therefore, also refrain from treating seed and fruit (and aggregates) separately in each chapter. A drupe and a berry repeat the functional structure of the seed of *Ginkgo*, *Cycas*, *Encephalartos* and *Magnolia*. It is, therefore, illogical to speak (as is usually done) of the seed of *Cycas* as drupelike. As I have said, considerations on homology in fruits and its precise analysis are for the time being superfluous in ecology, a discipline which works with convergent organs and tissues. A drupe then answers the old description in the classical *De fructibus et seminibus plantarum* of Gaertner (1788–1807), irrespective of the homology of juicy and protective parts. In an effort to bring in homology as a tool for defining fruit classes in a system, Takhtajan (1959) distinguished between drupes from inferior and superior ovaries. This distinction is not only ecologically superfluous but also morphologically in-

sufficient. Inferiority of the ovary is based on divergent morphological conditions (occlusion by either axis parts or appendicular parts). And, worse, it is not "pure" morphology (if such morphology is possible at all), since inferiority is a convergent ecologism in the flower phase (see p. 19). In some drupes of Santalaceae the kernel arises from the mesocarp, not from the endocarp.

Also in seeds we find functional convergence of histogenetically different layers, clearly in the protective (palisade) layers, and apparently also in other specific organs as tapetum and sarcotesta. Even the homology of all integuments is sometimes doubted. For mucilagenous layers see p. 78 and p. 116. For such shifts in general p. 145.

## B. Morphological Fruit Systems

In spite of these and other objections, various authors have considered it possible to construct systems of fruits on a morphological basis. Attempts were made by Winkler (1939, 1940) and Baumann-Bodenheim (1954). It has also been thought possible to construct systems on a double basis: viz. first the "general", "morphological", ecologically neutral basis of the carpels and their coherence, and secondly the refinements occasioned by the ecological requirements of dehiscence, consistency, etc. Many Eastern European systems reflect this attitude: Goby (1921), Gusuleac (1938), Hegedüs (1948), Takhtajan (1959) and Kaden and Kirpichnikow (1965). Worthy of special note is the system of Levina (1961). All these systems shower us with a deluge of new terms (hundreds) not to be cited here, and merely providing compilers of future glossaries with Parkinsonian work. In the Eastern European systems, the morphological bases are indicated as "genetic", meaning in this world of thought "ontogenetic". The deeper morphology of the constructional parts in ontogeny is either neglected or considered at the classical level of Goethean simplicity and typology. The line of development described in them is typological on a basis of monophyletic angiospermy. To mention an instance, the absence of septa in monolocular fruits can be read in two opposite senses or be explained on the basis of the revolutionary concepts of the New Morphology (Meeuse, 1966 e.s.).

## C. Morphological Interaction Between Fruit and Flower

### 1. General

There seems to be a lack of coordination between flower and fruit when fruit trees produce thousands of perfect, entomophilous flowers, when they can nourish only a few of the ensuing, very large fruits. One might consider this numerosity as enhancing the chance of pollination, but normally they may drop more than 99% of the pollinated ovaries (cf. *Mangifera* and *Parkia*), where, however, some flowers are only polliniferous.



That fruits can also lead a life of their own in diversification is demonstrated in detail in Chapters IX and X.

Morphologists should be extremely careful when dealing with the fruit, the youngest organ of an ecological nature, where function is dominant and causes endless convergence. On the other hand it may seem strange that not the final organ, but an intermediary one (the flower) has to form the basis of classification. But what is final? I have other fundamental objections to the principle of adopting a morphological basis for fruit systems. One is its inadequacy with regard to the pluriformity which exists in groups such as the Leguminosae (see Chapter IX), where the simple and uniform ovary produces a world of forms and where pure morphologists must feel like deaf people arguing about music.

Another objection is that the fruit morphology cited refers in essence to the ovary and thus to an organ of the flower, an organ for pollination not necessarily bound to functions of the fruit. I do not understand how Esau, in her textbook of plant anatomy, could postulate that the classification of fruits should reflect the structure of the flowers. Flowers in what phase? The function of the flower in all stages, containing three generations (old diplont, haplont and new diplont), is of a triple nature: first spore production, then fertilization of the haplont with embryogenesis, finally the main function, the formation of seed and fruit. The different spheres of life remain in this contraction nevertheless more or less separate in their functional adaptations.

There is, however, interaction due to a shift in time of morphogenetic processes. The anatomy of an ovule can be influenced by the later function of the seed. A vascularization of the integument may be just a prelude to a special testa, such as the sarcotesta of *Magnolia*, Euphorbiaceae or Sapindaceae or the watery, viviparous testa of *Hymenocallis* (see p. 118 and p. 136). For other cases see p. 65. In *Crinum* the absence of ovular integuments is connected with later vivipary. In *Melocanna* it allows the nude, viviparous embryo to feed on the pericarp. The queer venation of the carpel in *Nypa* can be a prelude to its special fruitwall. The early penetrance of dispersal genes in *Acer* leads to an excessive ovarial wing before and without pollination, that apparently caused the flower to choose between formation of either stamens or ovary (dicliny). Often a mental analysis is necessary to decide for what sphere of life a constructional detail can be interpreted as adaptive and to which one it can be assigned in terminology. This differentiation in terms is not a mere play on words, but is necessary for the correct insight into the nature of things to be compared. The often-committed sin of interchanging terms for the flower and the fruit hinders, as will be shown, insight into the interaction and into the backgrounds of taxonomic and phylogenetic relations. We shall later see how misleading the unfortunate use of the seed-term "angiospermy" for the flower has been.

Some interaction between pollination and seed dispersal (between flower and fruit) seems, however, unavoidable in an organ serving both processes. Anticipation of the dispersal function is sometimes found in transformation of the calyx in female flowers only. In anemochorous-hydrochorous *Gyrocarpus* (Hernandiaceae) it is already winged. For the utricle of female *Carex* flowers and for

awns on only female grass spikelets see Chapter X. Such dimorphy may be behind many cases of dicliny (next to other influences). Burt (1961) indicated this interaction in the heads of Compositae, which also serve two functions, the pappus and involucre being most active for fruiting. Zohary (1950) had already pointed to the two distinct evolutionary trends in them, as discussed under heterocarpy on p.98. Epizoochory of fruiting heads can be expressed only in the involucre and in the reduction of the number of florets (p.99). Where there is interaction, I shall indicate the residual influence of the flower phase on the seed or fruit as postludial and the reverse, anticipative influence as preludial. Sometimes a fourth sphere of life, germination, can prelude in flower, seed and fruit.

Considerations on interaction should not overlook that an ontogenetically late organ in the flower is often phylogenetically basic. The matter is treated in some detail in a separate study (van der Pijl, 1978).

## 2. Position

The terminological differentiation of characteristics is evidently necessary in regard to the position, the place of presentation. We find a special position on the trunk and on dangling long stalks in bat-flowers (see Faegri and van der Pijl, 1979), also in bat-fruits (see p. 50). In flowers, we have to call the phenomena "cauliflory" and "flagelliflory" respectively, in fruits or seeds "caulicarp" and "flagellicarp" ("flagellisperm"). The interaction between the two phases is evident when there is no postfloral change in position [as there is, for example, in the dangling seeds of *Swartzia* (p. 52 or the dangling fruits of *Mangifera* (Fig. 12)]. The non-chiropterophilous flower can already, as a prelude to the caulicarpous bat-fruit, be situated on the trunk, although at first sight this "does not seem to make sense". This is the case in *Ficus* spp. with pollination by wasps, for whom the position is unimportant. The reverse is the case with the non-chiropterophilous fruit which as a postludium remains on the trunk when its flower was more or less cauliflorous for pollination by bats. This is presently the case in *Durio zibethinus*, where the fruit is dropped before dispersal, thus being nonfunctionally caulicarpous. The plant species is cauliflorous. In *Artocarpus heterophylla* (jackfruit) we meet a convincing refinement. The position on the trunk concerns the female inflorescences only and appears thus as caulicarp, useful for bat dispersal and the bearing of very heavy fruits. See further pp.27 and 50.

The adaptive positioning of ant-fruits near the ground (see p.57) can be performed by postfloral changes of the flower stalk, but can also be precluded in the flower, as Sernander (1927) remarked. He even found consequences of this in the flowers of some species of *Geranium* and *Veronica*, i.e. in a reduction of cross-pollination correlated with a deviating fruit ecology. In geoflory and geocarp the changes in position between flower and fruit are better known. *Arachis* even shows two opposite elongations. The flowers are placed low, and the attractive parts are brought upward by an extremely long hypanthium or perianth tube, quite exceptional in Papilionaceae. This tube wilts postflorally and the unstalked

ovary then develops a stalk which pushes the fruit into the soil. In *Colchicum*, *Crocus* and other geophytic monocotyledons the fruit moves in the opposite direction. The plants provide as a functional flower stalk a parallel perianth tube, leaving the ovary underground until the stretching in the next season, which is more favourable for the seeds. In some the tube also functions for moth pollination.

When we discuss the ecology of periodic fruiting it remains necessary to consider that it may be a mere consequence of periodic flowering induced by an external cue or not. Feedback by selective forces must, however, also be envisaged.

### 3. Monovuly and Monospermy

The number of seeds and ovules depends on the interaction between flower and fruit. The reduction to one ovule has to be indicated as monovuly (as distinct from monospermy). It is adaptive for anemophily, very clearly so in families with habitual polyovuly and entomophily, where one species has become anemophilous and monovulous. Monospermy is clearly adaptive in plants with indehiscent dry fruits and drupes. It is one of the ways of escape from angiovuly (pp. 133–135). In grasses monovuly and monospermy are both functional, the first seeming to be primary as a consequence of wind pollination (see Faegri and van der Pijl, 1979). For the aspect of dispersal here, see p.33 and Chapter X.

In Fagaceae monospermy seems primary with regard to the production of nuts and acorns, monospermous fruits with large seeds, which have an adaptive value in the rain forest (see p. 105). The correlative reduction of the ovule number seems a prelude interaction. Primary monovuly seems excluded, since the basic tropical oaks and chestnuts are still entomophilous (old cantharophily as described in Faegri and van der Pijl). We may even assume that this secondary oligovuly paved the way to their later, partial anemophily which is almost exclusive in temperate regions. We see that an adaptation in one field can start a new radiation in another field.

Since the character “ovules few” can be either carpal or floral in origin and nature, it cannot be used as such in statistical comparisons. Protagonists of anemophily as basic in some angiosperms have to accept monovuly as basic and have to assume that polyovuly has been secondarily acquired in such groups.

We leave aside here the relation of seed size and seed number with insect predation (Janzen, 1969b and many later publications) and the relation of mast-fruiting to seed predator satiation.

### 4. Inferiority and the Calyx

Inferiority of the ovary is usually a floral character. In many cases it has been explained functionally as a protective device against gnawing beetles, which were the pollinators in early periods. The reasoning cannot be applied to cases of a more recent character, such as in Ericaceae, where inferiority by occlusion of the ovary inside torus and calyx appears in the genus *Vaccinium*. The envelopment

of the fruit proper by the calyx into a pseudoberry, so common in related genera and thus of a carpal nature, seems in *Vaccinium* to be anticipated in the floral phase.

In the Compositae too, however, we find as a first preludial influence of the later pappus the special transformation of the free, upper calyx parts in the floral phase. The curious late ontological differentiation of this calyx may be a remainder of this situation. A fuller explanation of possible anticipation in the composite calyx follows on p. 159. Here we meet again anticipation by dispersal genes in the formation of a pappus before anthesis and independent of fertilization and seed formation.

## D. Inadequacy of Current Fruit Terminology

Some fruit systems deviate from those indicated before as morphological. The one by Janchen (1949) is described as functional, as he thought it unwise to place fruits in a morphological straitjacket, although using morphological criteria and tending to neglect dissemination.

The current terminology and the fruit system used in handbooks and school-books stem from extensive reviews, as in the *Handwörterbuch der Naturwissenschaften* of which Pascher and Pohl revised the second edition (1934). It is, in principle, monstrous, as it uses diverse criteria indiscriminately: morphological, ontogenetic, histological, ecological and physiological. No wonder representatives of each of these branches have complained about the inconsistencies and inadequacies! The system characterizes anything that does not fit into it as "accessory". This category includes, as we shall see, a large proportion of archaic and tropical fruits. Moreover, the system is too European-centered, even in its terminology, focusing on pericarp fruits. Stopp (1950 and many subsequent papers) showed its insufficiency, but as yet no typological school has produced a complete system. I mentioned several more morphological systems before and must admit that I could not produce anything better if it were necessary in this book. The fruit is too versatile and has too many aspects to be divided into strict categories. The basic division into dry and fleshy fruits is no longer tenable (see below).

Even the conventional distinction between endo-, meso- and exocarp is only functional, often without a firm histogenetic basis. We shall study transference of function later, and here leave aside the endless complications of spurious fruits, but indicate some types of true fruits that need recognition and perhaps a name:

### a) Seeds dominant

1. Seeds attractive, pericarp early caducous
2. Seeds juicy, carpel opened early
3. Nude seeds dry, pericarp early open as a dry wing
4. Sarcotesta seeds in dry pericarp
5. Seeds arillate, otherwise as in 4

b) Seeds regressive, dry

6. Mesocarp hard, endocarp pulpos (partly under the hesperidium)
7. Mesocarp hard, endocarp dry, splitting off
8. Pericarp dry, placenta fleshy (see p. 145)
9. Pericarp fleshy, dehiscing
10. Mesocarp hard, endocarp consumed during maturation, exocarp fleshy.
11. Fleshy funicles caring for or contributing to pulpiness (cacti).



## V. Ecological Dispersal Classes, Established on the Basis of the Dispersing Agents

### A. General

The sequence in which the various classes in dispersal ecology are to be presented seems at first irrelevant, as each agent, in principle, has the same rights. The question arises, however, whether historically the different agents could and did exert their rights equally well. The sequence used in most handbooks, although neither logical nor historically correct, has found wide acceptance, so that I have to justify my own deviating order; the more so, as our chapter on evolution will prove the existence of a certain line of development which does not start with the anemochory or autochory often assumed to be basic. In Pteridosperms and Gymnosperms we shall find reasons to consider dispersal of seeds by animals to be dominant. The wind dispersal of some *Pinus* seeds is derived from the animal dispersal in large-seeded species. The concept of anemochory as basic goes back to Sernander (1927), who was probably misled by the prejudice of his time as well as by the special situation prevailing in Europe. Thus he was influenced by:

1. the one-sidedness of European Gymnosperms, as anemochores;
2. the neglect of Ranales as primitive;
3. a false analogy between seeds and wind-dispersed spores;
4. the false concept of basic wind pollination in Amentiferae and of the primitivity of this group;
5. the concept that small seeds are basic.

Autochory is clearly a late way out, of limited importance; to be sure, in discussions of the topic it is often placed in front, but this is done for nonbiological reasons (do-it-yourselfers first).

One might try to classify the subject matter pertaining to dispersal on the basis of the diaspores of the plants, but this does justice neither to the convergent ways of nature nor to its complexity. The only practical order is obtained by following Ridley, with the agent of transport as the criterion for the main classes. It should be remembered that in pollination ecology the same order was recognized as satisfactory after similar prejudices had been overcome.

As in pollination, we shall find for the classes a general set of characteristics called the syndrome, sometimes wide, sometimes narrow and precise. Again, as in pollination ecology, not all the features are necessarily present, a single one sometimes being sufficient and decisive.

Geneticists stated that not just single characters, but certain combinations are favoured by selection. These "adaptive peaks" represent an aspect of our ecological syndromes.

## B. Invertebrates

Entomophilous fungi and mosses established a regular contact with flies and herbivores transporting spores from one dung heap to another. In the dispersal of the much larger seeds which appeared on the scene later, the role of insects is almost negligible, although incidental finds are reported. The exception is formed by ants, also latecomers, but the connection between seeds and these animals is so special and comes so clearly on top of older connections that we have to preserve it for the last, as an afterthought of nature.

The much older termites are purely dystrophic, meaning that they destroy anything transported, except fungus spores. The old assumption that they may bring *Rafflesia* seeds under ground to host roots needs proof. The agent should also provide the wound in the root necessary for germination.

Dung beetles in deserts contribute to germination by burying dung with seeds. Scarabaeid beetles in Brazil were seen to bury palm kernels (*Butia*) to oviposit on them. Some escape from demolition by the larvae (Silberbauer-Gottberger, 1973), giving the only successful seedlings.

There exist old data on dispersal by snails, especially for strawberries. Müller (1955) paid some attention to this point, adding some cases of ornithochorous berries (tomatoes, among others) eaten by snails. Except for the case of *Adoxa*, added later by him (1967), all this seems incidental utilization, without much dispersal value.

We must, however, after assistance by Dr. Doeksen (Wageningen) mention earthworms as dispersers. Darwin ascribed such a role to them. Seeds have been found inside them and are mostly defecated underground. As in Europe orchid seedlings have been found inside their tunnels, such passage may provide the penetration into deeper layers and other conditions necessary for natural germination. The supposed role in this respect of the unwettability of the seeds was disproved by Burgeff (1936). Vertical displacement of pollen by earthworms has been proved experimentally. Other old data, from Beccari's (1890) book *Malesia*, are not to be neglected. Beccari suspected earthworms as dispersers of the small seeds of saprophytic orchids, Burmanniaceae, etc. I always wondered how saprophytic *Epirrhizanthus* proceeded to get its small seeds deep underneath the humus layer. Burgeff tried in vain to obtain direct germination, also of *Burmannia*. The unconfirmed case of South African *Isoetes* spp., spread by spore-eating worms, is of theoretical interest as an ancient possibility (Duthie, 1929). Fungus spores are indeed thus dispersed. Worms may act as an intermediary agent, leading to dispersal at greater distances when eaten by thrushes. For modern experiments see McRill and Sagar (1973).

## C. Fishes and Ichthyochory

Vegetarian fishes may eat any botanical material, including seeds and fruits. Some seeds are so attractive that they can be used as bait. The same is true for

the sarcotesta seeds of *Pithecellobium microcarpum* in Borneo. A popular Brazilian booklet by De Arago (1947) describes how fish (genera *Osteoglossum* and *Brycon*) are lured by the fruits of trees growing on the shores of rivers. It gives only vernacular names of the trees but, as far as I could ascertain, these refer among others to the genera *Ficus*, *Inga*, *Myrciaria* (Myrtaceae), *Arecastrum* (Palmae) and *Guatteria* (Annonaceae). Many species of *Inga* prefer riverine habitats.

Ridley mentions *Pandanus helicopus* in this connection, and also the seeds of *Nuphar luteum* and *Bombax munguba* as being eaten. Corner (1949) mentions fish eating the seeds of *Dysoxylon angustifolium* and *Aglaiia salicifolia* (Meliaceae), growing alongside rivers in Malaya.

The seeds of *Dysoxylon* are poisonous, rendering the consuming fish unpalatable. Considering this, and though dispersal is sometimes assumed, the fate of the hard parts inside fish is doubtful. True dispersal by birds is here more likely. Both seeds are dangling, coloured, provided with sarcotesta or aril.

All this may be merely incidental. On the other hand, there may exist a natural and regular bond between fishes and the swamp and riverside plants mentioned, especially in the regularly inundated areas in Amazonia, where glaciation could not prevent the persistence of archaic conditions in the refugia during arid periods, Huber (1910), who was the first to suggest this, found in the intestines of large vegetarian fishes piracanjuba (*Brycon*) and pacu (*Myloplus*) seeds and kernels of Palmae and species of *Lucuma* and *Alchornea*, the latter with sarcotesta. Kuhlmann and Kühn (1947) also mentioned Brazilian palmfruits, especially *Geonoma schottiana*, as a preferred food of and bait for those fishes; also the fallen pods and seeds of leguminous *Inga* species. The latter may, as in some other cases, be archaic remnants. The same holds for the leguminous seed of *Eperua rubiginosa*, also used as bait in baskets. The tree grows along creeks in Surinam. Large fishes swim up to the splash when a pod explodes with a bang and swallow the large seeds. In the seeds (also in those of *Inga*) the testa seems attractive, not protective. Protection seems, moreover, superfluous in these not truly hydrochorous but nevertheless waterdependent seeds. Fishes may then provide the upward transport so puzzling in mere hydrochory – if the seeds are not 100% chewed up.

Gottsberger (1978) elaborated the question in the field for inundated regions in Amazonia, studying 32 plant species in which diaspores were consumed by fish. In half of these cases the seeds remained intact and this group contained mostly those from the more primitive families. Some fish migrate to the upper reaches of streams where fruits grow more densely and where their ripening starts at the season of high water. In many cases fish seem again unaffected by seed toxins. The dropping at maturity is often typical (e.g. in *Annona hypoglauca*, where the seeds are not destroyed). The limits with polychory, saurochory and pure hydrochory remain, of course, rather vague. The latter method refers to (masticated) seeds of *Hevea* and other toxic Euphorbiaceae. As in *Dysoxylon* they do not repel all fish. Here along banks one *Cecropia* sp. (*membranacea*) has also special traits pointing to dispersal by fish, confirmed by seeds in the intestines.

The European literature is rather silent on natural botanical fish food, and some of it is inaccessible. The researches of Hochreutiner, often cited, are of little value. Carp are said to eat fruits of the hydrochorous grass *Glyceria*. Heintze (1927) reported diaspores of *Aponogeton*, *Nuphar*, *Najas marina*, *Zizania aquatica*, *Salacia grandiflora* and *Ficus tweediana* as being present in South American fishes, and the olive-like fruits of a *Posidonia* (Najadaceae) as being eaten by tuna fish in the Mediterranean. Some relations between seeds and fishes can, as said before, be incidental and have arisen secondarily. Some species from carnivorous groups of fishes may have switched to late fruits offered in their biotope. An instance is the silurid *Arius maculatus* in the Indonesian mangrove, which feeds on the fruits of *Sonneratia* (used as bait) and even got its native name from this tree. The same may be true of the floating fruits of *Genipa americana*, discussed on p. 144, which are used as fish bait in S. America.

Though water-burrs do exist (see p.73) epizoochory on fish seems to be excluded. On the other hand the liberated, pointed seeds of *Typha* have been found in the muscles of fish and adhering to their skin.

## D. Reptiles and Saurochory

In old days reptiles were (as companions of and successors to fish) the main dispersers. For relations with Gymnosperms see the chapter on evolution, p. 131.

Among modern reptiles few vegetarians are left: some turtles and tortoises, a few lizards. The famous Galapagos lizards may have been driven forcibly into this habit of saurochory, as Darwin suggested in his *Voyage of a Naturalist*. Ridley cited these and other cases, among which are *Genipa clusiifolia* (Rubiaceae), Ulmaceous *Celtis iguana* (eaten by climbing iguanas) and the rather hard alligator apple (*Annona palustris*), eaten by iguanas and alligators after having dropped off the tree. The latter also has sea transport. Kral (1960) reported the gopherberry (*Asimina pygmaea*, Magnoliaceae) as being eaten by terrestrial gopher turtles. Shedding immediately after maturity may be typical, as for ichthyochory. More *Annona* spp. show it. Nowadays arboreal vegetarian reptiles are rare and flying ones absent.

Dawson (1962) described in detail the importance of such reptiles for cactus fruits in the Galapagos Islands, pointing especially to the germination which rapidly ensues after defecation. The local variety of tomato can in fact germinate only after passing through a tortoise, but not through other animals (Rick and Bowman, 1961). In a Queensland riparian forest an aquatic tortoise is said (Legler, 1976) to watch under a large-fruited *Ficus* sp. for the fruits. As this dropping is limited to a certain hour of the day and to juicy fruits the mere "windfall", as is assumed, seems improbable. He described also a parallel case in Panama. Some Antillean terrapins are reported to live practically off the fruits of *Annona squamosa*.

The desert iguana eats whole plants indiscriminately. Klimstra and Newsome (1960) found mature seeds in box turtles representing, among others, species of



*Rubus*, *Fragaria*, *Prunus*, *Polygonum*, *Vitis*, *Diospyros* and *Morus*. They showed that the animals had a well-developed sense of smell and a special optical sensitivity for orange-red. A number of zoologists confirmed this and elaborated upon it in work on the sensory physiology of reptiles. The sense of colour is weak in nocturnal reptiles.

It is remarkable that in arid volcanic habitats of the Canary Islands the rubiaceous shrub *Plocama pendula* (also eaten by other animals) returned to some saurochory for its juicy fruits. An omnivorous *Lacerta*, relying on the fruits for its water, disperses the seeds in its feces. (In gardens it became a pest for tomatoes.) Barquin and Wildpret (1975) described this, pointing to the dangling to ground level on the slack branch system. In Madeira the same occurs with a *Lacerta* that even climbs up to flowers for nectar.

The oriental *Chromastyx* is comparable to the desert iguana.

Research in the Guyanas and Amazonia may reveal many more instances. I think especially of dropped *Inga* fruits. The seeds mentioned in all those cases seem a secondary selection of what is at present offered and accessible; it may be theoretically important, as pointing to some archaism, that relatively so many "ancient" Ranales and Rosaceae are present on the list.

It may also be important that *Fragaria*, *Rubus* and *Rosa*, although taken by birds, are not typically ornithochorous (because they possess smell); in southern Europe and the USA wild strawberries are popular with turtles. These can reach other fruits that are close enough to the ground. The dropping of fruits of *Morus rubra* (popular with box turtles) seems not fortuitous.

As a syndrome of characteristics of reptile fruits, we can at this point state that the fruits have a smell, may be coloured, and are often borne near the ground or dropped at maturity. A hard skin is no obstacle for turtles with sharp beaks.

For the Asiatic tropics we have only some vague indications and traces discovered by Beccari (1890). He had reason to believe that the primitive, odorous sarcotesta seeds (near the ground) of the low swamp palm *Zalacca* (*Salacca*) *edulis* are eaten not only by rodents (as seen elsewhere) but also by varanes and turtles. On the authority of Dyak helpers, he asserted that the large and hard arillate fruits of *Durio testudinarum* in Borneo are eaten by turtles, a belief expressed in the name. The native name for this and other basicarpous *Durio* species (durian kura-kura) points in this direction. Now, such a vernacular name might just mean "unfit for humans", but the names for the different *Durio* species are too specific for that (Kostermans, 1958). The specific native names (also referring to birds) cannot refer just to external likenesses.

The oily pulp of *Durio zibethinus* is used in Indonesia as bait to catch crocodiles – so I was told. Other wild species, which have red, dehiscent, not strong-smelling fruits, eaten by arboreal animals and probably also hornbills, do not drop the fruits.

Should the Durian Theory (cf. p. 139) of primitive fruits be extended to take account of reptiles? In this connection, the basal caulicarp or basicaulicarp (on the trunk near the ground) of *Durio testudinarum* and other spp. can be seen as

an adjustment to ground animals. Other archaic *Durio* species (as *D. oxleyanus* and *D. dulcis*) have axillar and simpler flowers, and drop their smelly fruits; on the ground these open by gradual decay (cf. *Degeneria* p. 135) and by exposing the edible coloured arillodes. This situation (Kostermans, 1958) seems impossible to understand without ancient connections with ground animals, originally reptiles but now also mammals. The armour prevents predation by small animals who are unable to swallow the seeds. Some species became ornithochorous, with red fruits, dehiscent with red exarillate seeds. The basicarpy appears to affect adversely the high-level pollination of some *Durio* species (by bats). In *D. testudinarius* such pollination has not become impossible, as Dr. J. A. Anderson (Kuching) wrote me, for in the area where this species occurs bats have been caught at the expected low levels in mist nets.

Sometimes such basicaulicarpy is described as just geocarpy, a term better reserved for other phenomena, with underground fruits (p.95). The term basicarpy can also be applied to other general phenomena (p.94) in herbs.

We shall discuss here other cases of comparable basicaulicarpy, also of long fruiting stalks creeping over the ground (sometimes called "rhizanthly"). The two connected phenomena occur combined in a number of old groups with primitive zoochorous fruits: Menispermaceae, Annonaceae, Flacourtiaceae, Sapindaceae, Dilleniaceae, Euphorbiaceae, Sterculiaceae; also in members of the old genus *Ficus*, already abundant in the Cretaceous. In "geocarpous" species of *Ficus*, the syconia are indeed more or less underground, a situation which is not demanded by the particular mode of pollination (by primitive wasps). The low position of flowers and fruits also stands outside the pollination sphere in some species of *Baccaurea* (Euphorbiaceae), such as *B. parviflora*, and in some species of *Stelechocarpus* (Annonaceae). There, only the female flowers are basiflorous (a situation without pollination function); consequently, the fruit is basicarpous, a situation with a dispersal function. Amazonian *Iryanthera juruensis* (Myristicaceae) seems comparable. The *Artocarpus* mentioned on p.18 may also originally have been saurochorous. The special position of their female flowers was stressed as early as 1910 by Haberlandt in a note on p. 292 of his *Botanische Tropenreise*. Other spp. (*A. teeculiane*) are said to drop their fruits at maturity, and from the Phillipines a geocarpous one is reported.

Besides the *Salacca* mentioned, other palms join in. *S. flabellata* (Furtado, 1949) even shows "rhizanthly". Such forms, branched in the rhizome, seem ancestral.

In a later chapter dealing with the geocarpy of desert plants (p.94), I shall mention, as parallel to *Plocama*, other rubiaceous cases which descriptively seem to belong here. It demonstrates the danger of descriptive, indiscriminating terminology without appeal to function!

A number of papers on saurochory by Borzi (amongst others 1911) were inaccessible to me. In contrast to theories on the origin of Angiosperms on mountains (see e.g. p. 148) we may refer here to theories stating stream margins as the original habitats.

We may expect no exo-(epi-)zoochory on smooth reptiles and thus the phylogenetic emergence of burrs had to wait for furred animals and for herbs. These burrs are lacking in simple Ranales too. Further discussion of the evolutionary aspects of the conditions just mentioned must be reserved for the special chapter. Let us, however, point out that when we call this kind of cauliflory archaic, this does not mean that it is restricted to unbranched, simple trees, or that it is archaic only in the meaning of "not to be understood" (Corner).

We enter here the more general field of zoochory, dispersal by animals. Before we proceed with further classes, we must recognize that in the question of transport, the "how" and "where" also count. All following zoochorous classes can be subdivided by crosswise partitions as follows:

- a) endozoochory, diaspores inside the animal;
- b) synzoochory, diaspores deliberately carried, mostly in the mouth (stomatochory) as in some birds and all ants;
- c) epizoochory (formerly indicated as exozoochory), diaspores accidentally carried on the outside.

Since epizoochory on various animals is not very different in character and since this partition splits off a group with typical characters, we shall treat this horizontal grouping separately, after the classes created according to agents. This inconsistency (not maintained everywhere) may be forgiven because it yields practical results. Some endozoochorous fruits are dispersed each by various kinds of animals, but here inclusion in one class would delete fundamental differences.

## E. Birds and Ornithochory

The following subclasses can be distinguished:

1. Epizoochores
2. Synzoochores ———— 

stomatochores  
dysozoochores
3. Endozoochores ———— 

accidental  
adapted

edible diaspores  
mimesis

### 1. Epizoochory by Birds

There are two reasons for dealing with this group separately here, even though birds rarely transport burrlike diaspores, as observations show and as their preening habits suggest. Moreover, birds living high up in trees have little chance of meeting spiny diaspores. In the tropics of both hemispheres there exists one notorious genus of trees, *Pisonia* (Nyctaginaceae) with very sticky fruits. Large birds can be covered by them and severely hampered in their movements, while small ones can be immobilized until they die. *Cordia* fruits can join in. There is proof that distant islands can be colonized by viscid and barbed diaspores with

the aid of large sea birds (cf. *Remusatia* on p. 12 and the subchapter on island floras). Especially during breeding diaspores can penetrate into the plumage. Many species of *Pisonia* are found on Pacific islands, and burrs of *Acaena* have been found on migrating petrels arriving in oceanic islands.

The most frequent method, however, is by means of small, unadapted diaspores present in the mud sticking to the feet of waterfowl. Darwin investigated this, collecting and sowing the diaspores. Ridley devoted seven pages to examples – species of *Juncus*, *Carex*, *Polygonum*, *Glyceria*, *Cyperus*, *Alisma*, *Hottonia*, etc., describing cases of the sudden appearance of such plant species along the margins of isolated ponds. On p. 549 he gives an enumeration of small-seeded plants possibly brought to islands in this way. He pointed especially to the liberated, viscid seeds of many *Juncus* spp., which are rarely hydrochorous and accordingly do not show the monospermy and occlusion of the fruit of the original Gramineae and Cyperaceae (cf. p. 161). The (apparently more recent) anemophily of *Juncus* has not yet caused monovuly.

This accidental transport (also by mammals) is often placed under “chance dispersal”.

## 2. Synzoochorous Bird Diaspores

First we present the case of the edible diaspores of *Viscum album* carried in the beak, in which the viscid seed is reported to be immediately redeposited when the bird whets its bill on branches. This was said to be done regularly by mistle thrushes (*Turdus viscivorus*) specialized to some degree on the fruits; however, most of the seeds are just regurgitated from the gizzard or pass completely through the animal (endozoochory). The viscid part of the endocarp makes for ideal dispersal, viz. to the right substrate, with establishment ensured. Other birds join in. Some destroy or kill the kernels. In most instances the pericarp is eaten whole. In North America species of *Phoradendron* are dispersed by various birds (McAtee, 1947).

Many birds are alleged to act as dyszoochores (Müller-Schneider, 1955) when they eat diaspores and digest them. Thus, wood pigeons are reported as dys-trophic to *Fagus* and *Quercus*, but they disgorge or drop some of the “nuts”, thus contributing to regeneration.

Thrushes, waxwings and crows can disgorge large seeds and kernels, as toucans do with the large stones of palms (*Euterpe*). This process is a transition between syn- and endozoochory.

Real synzoochory of a partly dyszoochorous character results when nut-collecting birds cache part of their food or place it somewhere to be pecked, but neglect to eat it. The survival of diaspores in this case seems entirely accidental and incidental, but when this happens regularly to even a small percentage the method can be regarded as the normal dispersal mechanism for many plant species, just as wind dispersal, which also involves great losses, is the normal mechanism for pollen of wind-pollinated flowers. For large diaspores with relatively difficult water absorption the burying is also essential for germination, as



has been proved for acorns. So this wasteful, low-quality method has a high-quality aspect. Largeness must make the diaspores worth storing. Presumably "lost" seeds can (like spilled or stolen pollen and nectar) in other respects maintain the biosystem as a whole with feedback to dispersal agents. For seeds, the method described must have started in Gymnosperms (large *Pinus* and *Araucaria* seeds in Europe and America) (Swanberg, 1951). *Pinus cembra* is actually spread in this way by squirrels, woodpeckers and nutcrackers in the Alps near the forest limit, and depends on burial by them in the Siberian taiga, where almost all herbivorous vertebrates feed on its seeds. Best known for this method among the animals are the nutcrackers (*Nucifraga*), feeding largely on "nuts" (*Fagus*, *Quercus*, *Juglans*, *Castanea*, *Corylus*). *Garrulus* species (jays) and rooks have been observed to bury hazelnuts and acorns (Chettleburgh, 1952). In North America the pigeon *Columba fasciata* (eating seeds of *Quercus*, *Pinus*, *Prunus*) and even some woodpeckers are considered as forest planters (McAtee, 1947). The California woodpecker (*Balanosphyra*) can imbed thousands of acorns, almonds and pecan-nuts (*Carya*) in bark fissures or in holes made in the bark. This dyszoochory rarely has a dispersal effect, but rodents may steal the imbedded diaspores and store them underground. Schuster (1950) gave a fine description of the activity of *Garrulus glandarius* in Germany, where on the average each bird transported 4600 acorns in one season. Many birds flew with them to a forest at 4 km distance. Later on, distances of over 10 km were observed. The average is much less, but extremes do count here. Müller (1955) gave a detailed review of these cases. The occurrence of beech trees in groups is ascribed to such caches. I go into this matter somewhat more deeply because of the doubts of Webb (in Hawkes, 1966). He challenges the effect of rooks carrying acorns and finds no correspondence between the time (2000 years) the mixed oak forest took to spread over the British Isles (assuming that it started in southwest England so that each generation of 20 years had to advance 60 miles) and the dispersal possibility, excluding man. Friends have pointed out one bug, viz. that Webb has included a miscalculation. His result should have been 6 miles per generation. I might add that migrating nutcrackers and regurgitating pigeons may have provided steps larger than the 4 km mentioned above.

However, one should not be rash in blaming ecology as being "defective". The bedbug was used by Webb as a comparison, being well known for having no wings but getting to places nonetheless. Being familiar with hygiene, one has to admit that it is possibly carried by man. The bug may also be on the premises!

The remark by Darwin that even birds of prey may provide secondary and distant dispersal after slaying other birds, was confirmed by Balgooyen and Moe (1973). They found viable grass seeds in regurgitated pellets of *Falco sparverius* in the U.S.A.

*Aesculus hippocastanum* could not follow the retreating ice in Europe and failed to regain its old territory in the North mainly for lack of finding (new) disseminators, as *Quercus* did. Wild boars are probably purely destructive for all diaspores discussed here. Dr. B. J. D. Meeuse (Seattle) informed me that in the U.S.A. grey squirrels overcome the saponines in *Aesculus* seeds and store them.



In considering *Quercus* and *Castanea* and their difficult dispersal, one should not forget that the genera were originally at home in the humid tropics, where a large seed is more important than a fast seed (p. 105). A study of their dispersal there is sorely needed, as we have only a few data on nibbling squirrels (Ridley, p. 377).

In cases of biotic dispersal, the synecological aspect should be taken into account, i.e. the fact that the biotope in unconquered land should fit the dispersing animal. A jay has no natural disposition to cache acorns in a distant, open heath.

Telegraph wires may promote seeding in open plains. After a phase of abiotic dispersal of pioneers the first berry-bearing plants, brought by incidental droppings, can accelerate revegetation into forest. They provide food for regular visitors and change the biotope to the needs of fruitbirds (and especially for fruitbats). As we shall see, a mixed diet of the bird and its nesting in outlying territories, also the presence of preceding trees with a mixed dispersal or with mixed attraction (*Pinus* species) can aid in the accessibility of the region to birds. The substrate should, of course, also be in the condition required for establishment.

The historical checking of dispersal can in this book only be touched upon here and there. The subject lends itself more to writings of a geographically limited scope. For postglacial history in Scandinavia, I mention the investigations of Firbas (1935) on the shifting, with time, of the distributional limits of some forest trees. For *Alnus*, *Betula* and *Corylus* these agree with the findings of dispersal ecology; for *Pinus sylvestris* and *Ulmus montana* they exceed regular possibilities. Müller (1955) suggested here some influence of exceptional dispersal, not of a community but of a pioneer. Incidental accessibility of the habitat and the reverse, the occurrence of barriers, play a role here, as is obvious in the Alps, where descent into valleys was easy.

### 3. Endozoochory

**Non-adapted Diaspores.** We might start with the most primitive method, the indiscriminate swallowing of diaspores together with foliage, but in this case the possibility is just theoretical.

Next comes the mainly dystrophic, dyszoochorous action of granivorous birds feeding on dry fruits and seeds. This class is not always distinct from the synzoochorous one described on p. 29 and the one regarding fruit eaters (see for instance, crows). The seeds or achenes are often shelled in the beak and ground so thoroughly in gizzard and stomach that they are destroyed. Agriculturists considered the activity as favourable for getting rid of weed seeds. Old countings of Kempfski for pigeons and hens gave in regard to *Lithospermum* and *Rumex* that 4% of the seeds passed intact, of which 25% would germinate. Recent research on the droppings of pheasants, crows, sparrows, wood pigeons and starlings showed that the percentage may be higher. See also Ridley (p. 439) and Krefting and Roe (1949). Ridley (p. 440) already remarked that granivorous birds contribute considerably to the dispersal of seeds classed otherwise, as of grasses, *Bellis* and



**Fig. 2.** Dehiscent follicle-pod of *Archidendron vaillantii*. (Bailey-Compr. Cat. of Queensland Pl.)



**Fig. 3.** Dehiscent fruits of *Paeonia mlokosewitchi* with smooth, blue, fertile and wrinkled, red, sterile seeds, both juicy. (Photo Natan)

*Plantago* (sold as birdfood). Toxicity seems confined to seeds from other ecological classes, that are not digested. The point (toxicity is always specific and relative) deserves attention for small "seeds" of Leguminosae, falling into this ecological class (see p. 157).

Immigrant granivorous birds (*Plectrophenax nivalis*) of a non-Icelandic race were caught on the new island of Surtsey off Iceland. Their gizzards contained viable seeds picked up in the British Islands (Fridrikson, 1969).

Ducks and other water birds swallow large quantities of seeds, mostly those dropped into the water, also sunken ones obtained by diving (For *Zostera* see p.73). A part remains intact after regurgitation or defecation. For *Carex* see Birger (1907). The lack of colour is no impediment for the (often nocturnal) birds. The residual monospermy of Gramineae and Cyperaceae may originally have led to the combination in the diaspores of hydrochory and endozoochory that will be discussed in detail in Chapter X. For the hydrochory see p.75. Ridley gives six pages on different species, stressing the influence of their migrations on plant dispersal and distribution. This is most important for Cyperaceae, but also for species of *Nymphaea*, *Nuphar* and *Pontederia*, and even for some plants with berries. For *Potamogeton* see p. 123 for the clear zoochory in cyperaceous *Gahnia* see p. 44.

The residual monospermy of grasses (p.19) may originally have led to the combination of hydrochory and endozoochory (as seen in Cyperaceae), promoted by enclosing, utricle-like glumes. This condition in Oryzeae may be just as original in the family as their flowers appear to be, and may explain the general reduction of pericarp and testa in the family. In some bamboos (also with primitive flowers) the pericarp remains of some importance (see Chap. X).

De Vlaming and Proctor (1968) investigated experimentally and quantitatively the periods of retention and the relative viability of many aquatic diaspores inside some shore and water birds. They confirmed many old positive assumptions about this type of dispersal, but emphasized the limitation to small hard diaspores, apparently more or less (pre-)adapted in this respect, perhaps collateral to hydrochory (thus diplochory). This limitation applies to some Cyperaceae and some species of *Potamogeton* and *Sagittaria*, where often dispersal over far more than one thousand miles by widely migrating waterfowl (and increased germinability) seems ensured. Such dispersal means a large loss of diaspores, but this is counterbalanced by directed dispersal to favourable sites. Good quality of dispersal again compensates for low quantity. Proctor's data (1968) augment the possible times and distances for different, upland, seeds. This is not the place to discuss migration routes of birds over the oceans in detail.

**Adapted Diaspores.** The bulk of the ornithochores have diaspores adapted to fruit-eating birds, which excrete the hard part undamaged.

Here too one should be reticent in relying on superficial observation of feeding. Some protein-loving birds (e.g. tits) have been reported as taking also berries and drupes, but are dyszoochorous, since they destroy the seeds. *Coccothraustus*, the hawfinch, has been given for this reason the melodious German name of

“Kirschkernbeisser” (“cherrystone destroyer”). Parrots too are destructive. They destroy seeds, ripe or unripe. Frugivores that strip off juicy parts at the spot are poor dispersers. As a consequence of having fruitless periods, temperate regions possess few birds which feed exclusively on juicy fruits. Few fruits (*Prunus*, *Ribes*) mature in summer there. Ridley relates (p. 455) that in North America, where soft fruits are more abundant than in Europe, the native crow is more of a softfruit eater. Wood pigeons, preferring acorns and beech-mast but accepting cereals, later switch to berries (as documented in the case of *Ilex* and *Hedera*). Thrushes switch from insects, etc. to fruits. Some of these (*Hippophaë*, *Berberis*, *Rosa*) are accepted by them only late in the season, in some regions not at all, so that the fruits have to rely on wind dispersal when dry. Many (*Juniperus*, *Cotoneaster*, *Hedera*, *Sorbus*, *Cornus*, *Ligustrum*) last through the winter locally as “winterstanders”, being consumed in a certain sequence. We know too little about competition between plants for dispersers and about specialisation. Müller (1955) lists a number of berries never consumed in Central Europe, probably because the natural specialist birds have become rare. Some of those fruits (*Berberis*, *Hippophaë*), less popular with resident birds (also in Kew according to Ridley), seem to rely mainly on migrants in winter. These are, for *Hippophae*, *Bombycilla garrulus*, *Turdus pilaris* and *Turdus musicus*, mainly along the coast. In Central Europe *Pyrrhocorax alpinus*, descending in winter from the Alps, then collects them. Competition between fruits plays a role in this respect. *Sambucus racemosa* is ignored by birds in certain years. Schuster (1930) and Birger (1907) gave an interesting list for Europe. Much literature on bird dispersal in North America (94 items) has been compiled by McAtee (1947).

Pure fruit-eaters can form a permanent part of forest ecology in the tropics, as described on p. 103. Some belong to the thrushes and pigeons, having different tastes there and swallowing larger kernels than in Europe. Many fruits in southern regions have a higher content of lipids and proteins. This is especially important for those birds where the nestlings are also fed on fruit (see the oilbirds on p. 38). Such absolute frugivores, therefore, select such rich fruits already present as an old family character amongst Palmae, Burseraceae and Lauraceae. Oil was always a general attractant in reptile diaspores, now also for other animals. See also *Persea* on p. 54. Such birds can be contrasted with fruit generalists such as Bucerotidae and Capitonidae (p. 35), which add animal food to their diet, also for the young. Snow (1971) considered such evolutionary aspects.

The paper by Philipps (1926), quoted extensively by Ridley (p. 499), gives details on African birds. I quote many *Olea* and *Elaeodendron* spp., the oily fruits of which may be carried for miles by birds. In Indonesia the fruit pigeons (*Carpophaga*) played a role in history by eating nutmeg (*Myristica fragrans*) with its arilloid (the mace) and disseminating it outside the region set aside for its culture by the East India Company, with nasty results for the innocent inhabitants. They pass seeds and kernels through the specialized gut, also the large, greenish drupes of *Canarium* and *Elaeocarpus* spp., both containing oil and belonging to Burseraceae and Tiliaceae respectively. Actual dispersal by such frugivores is always said to be normally limited by fast evacuation (sometimes after half an



hour), but it may have played a role in some Pacific islands, as shown by the case of *Myristica*. Many showy ariloid seeds are present in the tropics, even among Euphorbiaceae, as shown in Chapter VIII.

The tropical family of flower-peckers (Dicaeidae) is specialized on Loranthaceae in a double respect. Its representatives take nectar from the flowers and have gizzards with a special structure, allowing the seeds to pass through, whereas insects are retained. The rind only is rejected from the bill. Long strings of excreted seeds infect trees (see Fig. 6). Docters van Leeuwen (1954) wrote an extensive monograph for Java. Other birds participate. High-quality dispersal!

Here we find real co-evolution with specialized birds (not even absolute frugivores), but the absence of a testa seems primarily due to their parasitism on branches, not to the sometimes mentioned, connection with "friendly guts". The birds also eat other fruits. The loranthaceous root-parasite *Nuytsia* has dry, winged fruits.

Seeds even larger than those of *Myristica* are devoured by Ratites. Other important tropical fruit-eaters are the barbets (Capitonidae), toucans and hornbills (Bucerotidae). The latter also swallow large diaspores, such as those of *Areca*-palms and the arillode seeds of *Afzelia* (see Fig. 10), also the berry-like exposed seeds of *Sterculia parviflora* (McClure, 1966). Figs form the main part of diet. Large seeds are regurgitated.

Mrs. G. Verhey (El Arish, Queensland) found in the excrements of cassowaries the large fruit kernels of *Pandanus pedunculatus*, *Elaeocarpus grandis*, *Davidsonia pruriens*, *Pleiogynium solandri* and wild mangoes.

Nowadays seeds of some Cycadaceae (*Zamia* and *Macrozamia*) are dispersed by birds, the latter by emus. These are reported to provide better germinability than mammals after passage of the same hard kernels (Noble, 1975). They replace mammal herbivores locally.

Many ground birds, e.g. tropical *Tinamus*, specialize in fallen fruits. Such birds are not necessarily low-grade dispersers nor are the diaspores (cf. p.39) low in adaptation. Both simply found a special niche in the ecosystem.

**The Syndrome of Bird Diaspores.** Birds have only a weak sense of smell, or none at all, and are visual animals. Birds can climb and fly but have no teeth. The botanical answer is that diaspores have:

1. an attractive edible part;
2. an outer protection against premature eating (green/acid);
3. an inner protection of the seed against digestion (kernel, bitter or with toxic substances);
4. signaling colours when mature;
5. no smell (although smell is no impediment when present);
6. permanent attachment;
7. no special place for the whole;
8. no closed, hard rind;
9. in hard fruits the seeds exposed or dangling.



Just as in the pollination classes of flowers, any individual feature can be lacking. Specialized birds are perfectly capable of finding greenish fruits, but the ideal case is a brilliant diaspore, with contrasting colours, preferably assisted by coloured auxiliary organs. Some *Sterculia* fruits look like two-coloured flowers. Those of some *Archidendron* spp. contrast blue-black berry seeds against the red (outer side) and yellow (inner side) of the valves.

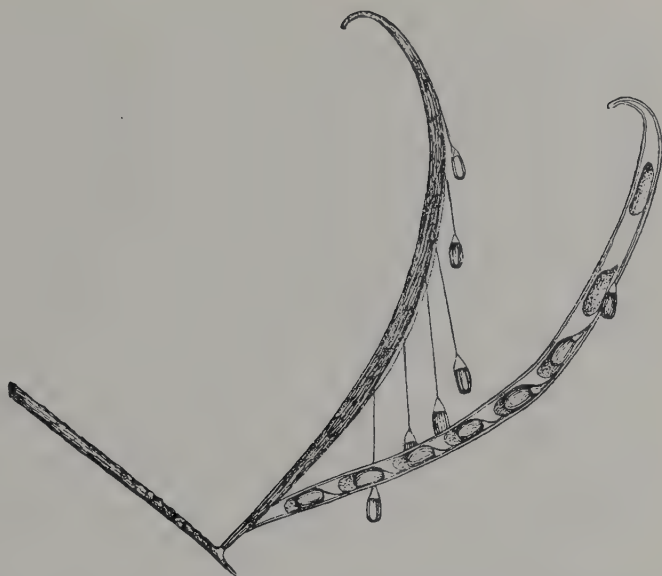
In *Ochna* the torus and in many *Clerodendrum* species the calyx provides contrasting colours, as do red arils on black seeds. In the simplest cases, as in *Magnolia*, only the coloured sarcotesta seeds are showy. Additional edible parts are numerous, as will become clear in Chapter VIII. In the giant cactus (*Carnegiea*) birds eat the seeds with the surrounding pulp. In many cacti this consists of juicy, swollen funicles, wound around the seed, and exposed by dehiscence of the fleshy pericarp. Just as in bird-flowers, red dominates. We are not sure whether this is based on the innate preference of birds, better perception, better contrast with the foliage, or the fact that the colour combination is a signal learned by association. The second best combination is black or dark blue with a lighter hue.

Two-coloured infructescences, as of *Viburnum opulus*, are conspicuous by the contrast between unripe red and ripe black fruits, of which the latter are eaten (see Ridley). In *Aechmea calyculata* (Brazil) the seedless fruits are red, the others black. In some *Paeonia* species (see Fig. 3) the contrast resides within one fruit, between sterile and fertile seeds, both juicy. Figures of such gaudy typical fruits and seeds can be found in Ridley's plates 15 and 16 and also in Hallé (1974).

The dimensions are usually smaller than in fruits for mammals (which possess teeth), but sometimes large fruits can be picked into fragments, or split open in spite of their fleshiness, as do some species of *Momordica*, *Gardenia*, *Fagraea*, *Cereus*, Lardizabalaceae. In the genus *Ficus* small coloured axillary figs are eaten by birds. The presentation of the diaspores proper on hanging funicles (or im-



Fig. 4. Seed of *Acacia falcata* encircled by juicy, folded funicle



**Fig. 5.** *Acacia australis*. Woody pod dehiscent, seeds on threadlike funicles with swollen tips. (After Velenovsky)

provided organs) can be observed in species of *Acacia* (see Fig. 5 and p. 152), *Magnolia*, *Xylopia*, *Eremurus*, *Anthurium*, *Gahnia*, *Euonymus*, *Xanthoxylum*. In other cases (*Archidendron*) (see Fig. 2) torsion of the valves provides exposure. In Australian *Acacia cyclops* (cf. Fig. 4) the ornithochory is evident (and confirmed) from the red juicy funicle contrasting with the dark seed and the persistent yellowish valves. This condition is missing in Africa (Middlemiss, 1963).

*Citrus* fruits (hesperidia) deviate from the ornithochorous type by possessing an indehiscent, repellent, tough pericarp and by the large seeds, which separate easily from the sweet pulp when pecked at. I found no data on dispersal in their natural environment. Ridley, however, cited data from Jamaica, where an *Icterus* and a turtledove feed on the fruits and cause spontaneous growth of seedlings. The type fits better to monkeys. In northern Australia cockatoos destroy *Citrus* fruits for the sake of the seeds. Some seeds may escape destruction after transport.

Temperate weeds are as a rule not truly ornithochorous, but there exist some weed-like shrubs and trees that spread rapidly through regions by means of birds. Bews (1917) described for South Africa the role of birds as almost the only agents of dispersal in the succession in the "thornveld", the phase after the grasses and before the establishment of trees (see p.48). In this intermediate phase almost no further anemochores appeared.

For the succession on the island of Krakatau see p. 109. In Europe, *Prunus serotina* has become a nuisance in woods. In Java, *Lantana* conquered open

country in a few years; in New Zealand and Brazil, species of *Rubus* did the same.

**Oil-containing Fruits.** We have already quoted a certain range of preference according to the taste of birds. This is obvious in the case of oily pericarps, sometimes also containing proteins. Oil in edible attractants may be primary, older than mammals and birds, present in arils on reptile diaspores (see e.g. *Durio*). Replacement by carbohydrates, especially in the north, may be secondary, as less expensive and faster in deposition. The olive is eaten by crows and magpies, not true vegetarians. Likewise, fruits of wild *Olea* species in Africa are consumed by pigeons, but also by diverse mammals such as dogs and wild cats, so the oil can be said to bring the fruits (again) into the range of carnivores, as we shall also see in mammal-fruits (*Persea*). The same applies to the oil palm (*Elaeis*), which has a special oil squirrel (*Protoxerus*) of unknown dispersal effect; it is effectively dispersed by vultures. One of these (*Gyphohierax angolensis*) has such a preference for the fruits that in West Africa it is referred to as the palm-nut vulture. In an oil-palm plantation in Surinam a local vulture (*Coragyps atratus*) switched to the fruits, perhaps from local palm fruits. The famous oil-bird (*Steatornis*) in Central America also preferentially collects oil-fruits in its gizzard, some from palms (*Euterpe* and *Martinezia* species, *Jessenia oligocarpa*), some from *Lonchocarpus*



**Fig. 6.** Kernels of Lorantheaceae excreted on a branch by a bird (Dicaeum), germinating and connected by viscin. Large ones of *Macrosolen cochinsinensis*, small ones of *Viscum articulatum* (hyperparasite). (After Docters van Leeuwen)

and *Protium* species. Like bats, it feeds on the wing at night. The possibility of convergence with bat-fruits should be studied. The oil-bird may have a sense of smell (large conchae) and is known to use sonar. Those seeds brought to the caves (also for the young) perish. See Snow (1962).

Is this really the end of a line of fruit-eating or a more sudden derouting, as in the vulture? The Kea bird switched from fruits to sheep's fat (if stories are true) in New Zealand. Did former oil-birds perform the opposite shortcircuiting?

**Remarks on Evolution.** We have seen, and shall later document in detail, that ornithochory is normal in primitive Magnoliaceae and Leguminosae with sarcotesta and ariloids. In higher families with wind dispersal certain genera have switched back to animals (*Vanilla* in the Orchidaceae with indurate seeds and finally odorous). For Gramineae see p. 173. In the Compositae endozoochorous, ornithochory developed terminally in a few pappus-less genera with a fleshy pericarp or even fleshy bracts (*Wulffia*, *Clibadium*, *Milleria*). The ripe capitulum integrates into one compound fruit, which is swallowed by birds and bats. We shall see later how profoundly the calyx of Labiatae is sometimes transformed for dispersal, often being included in the functional fruit (Stopp, 1952). It is, therefore, no wonder that in the genus *Hoslundia* the calyx has become fleshy and coloured. In Urticaceae-Moraceae with anemophilous oligovuly the basic fruit-type seems to have been a small, dehiscent drupelet on forest herbs (see p.85), which is sometimes desiccated into an achene. It often returned to full endozoochory by means of intricate devices, syncarpy (with fruiting perianth, pedicel or receptacle), sometimes allowing megaspermy in forest trees. I am not informed on the geological time of emergence of fruit-birds, but the change from reptiles must have been possible when frugivory and also tree life corresponded (see p. 132). Some authors formerly connected a change in fruit types with the change from the arborescent habit to the herbaceous habit of modern times in temperate regions. Birds there are said to be reluctant to feed on the ground, so that ornithochory diminished in favour of other mechanisms. I have objections but they are not those of Bancroft (1930), who emphasized that dry fruits are frequent among amentiferous trees, which he considered to be primitive plants (see p.22). In Leguminosae the later switch to anemochory also occurred in high trees, as exemplified by Piptadenieae (see p. 152).

As in the field of pollination we saw before that connections in dispersal often repose on utilization of new cross-links in a pre-existing ecosystem, not primarily on concurrent evolution on the species level and certainly not on some plan behind both animal and plant species. This synecological view is illustrated in van der Pijl (1969). It will become especially clear in the following section, where the natural link reposes on ecological parasitism (the derouting of forces), popularly called "deceit". Such deceit is frequent in pollination, especially of archaic flowers and again of orchids.

Further co-evolutionary bonds could, of course, arise out of incidental bonds. They rarely attain the interdependence, discussed here, of Dicaeidae-Loranthaceae.

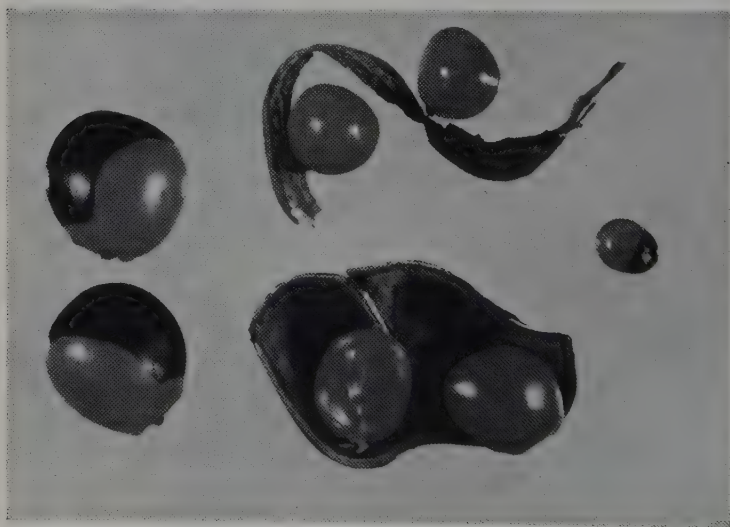


Interesting, but one-sided attempts of co-evolutionary considerations have been published by zoologists to qualify certain birds and their fruitfood as high or low in adaptation for dispersal. The strong specialisation of the oil-bird (p.38) means no high-dispersal quality. I point to the fate of most seeds here, to the limitation for plant dispersal to the bond of the birds to local caves and thus doubt of distances reached and of diffuse dispersion. The largeness of the seeds concerned means no high adaptation to ornithochory, but is just a consequence of belonging to the rain forest and to their respective families (see p. 105). Regurgitation in oil-birds is not their "high-quality" dispersal method which is assumed to be friendly to seeds consumed. This also occurs in low-grade dispersers (p.29).

Unadapted water birds distributed "low" Cyperaceae farthest over the world, the "high-quality" reposing on the common habitat. "Low" jays are successful planters. For "low" vultures see p.38.

**Mimesis (Imitative Seeds).** This part of endozoochory has such special features that I shall deal with it, and also (though Ulbrich denied it on his p. 135) the existence of "Täuschfrüchte", as a separate topic.

In entomology, the term "mimesis" or "mimicry" refers to imitative colouring of edible animals (usually insects) to avoid being eaten by predators (often birds). A distasteful animal serves as the model. In the botanical literature, imitative colouring of seeds is seen as a functional trick to obtain the reverse effect; edibility is suggested. In seeds, the term "mimesis" often refers to black and contrasting red colouring, a scheme also found frequently among the "warning colouring" of insects; however, the birds concerned with seeds are not pure insectivores and are therefore not repelled by this combination.



**Fig. 7.** Some mimetic leguminous seeds, of *Abrus precatorius*, *Ormosia dasycarpa* (both two-coloured), *Adenanthera pavonina* and another species of *Ormosia*. (Photo Natan)



**Fig. 8.** Dehiscent pods of *Rhynchosia mannii* (from a herbarium specimen) showing persisting, red corolla and mimetic seeds. (Photo Natan)



Certain tropical fruits produce seeds that resemble primarily the berrylike or-nithochorous seeds of *Magnolia* and *Archidendron* described on pp. 136 and 152, and consequently berries in general. Such seeds can deceive the visual birds. Feeding experiments by the writer in Java with the mimetic seeds of *Adenanthera pavonina* proved that granivorous birds refused them, whereas fructivorous birds (barbets) accepted them as berries, defecating them intact. Cockatoos tried to



**Fig. 9.** Dehiscent fruits of *Allium tricoccum* with mimetic seeds. (Photo Natan)

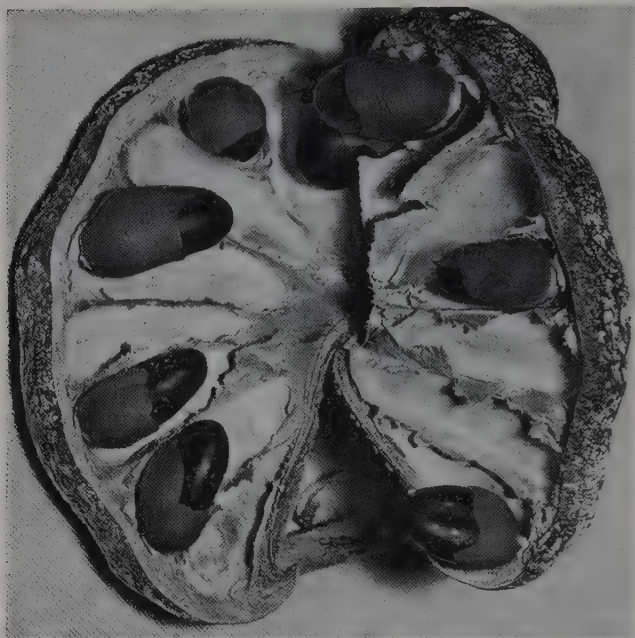


Fig. 10. *Afzelia africana*. Dehiscent woody pod. Seeds black with red arilloid. (After de Wit)

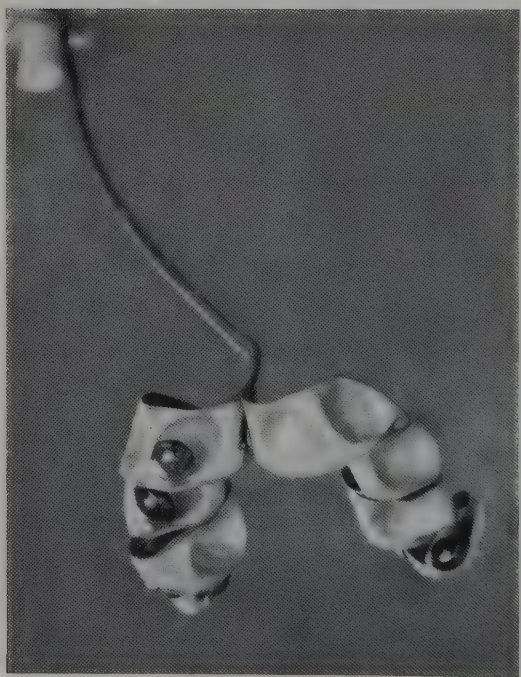


Fig. 11. *Adenanthera pavonina*. Dehiscent and twisted pod with attached mimetic seeds

crack the very smooth, hard and slippery seeds of *Abrus* (Fig. 7) with the tip of their bills but had no success and tried several seeds in succession, so that at last quite a number collected in the rear of the beak. Very young and wrinkled seeds were easier to destroy. Such red and black seeds seem to imitate arillate seeds, possibly even gymnospermous ones, as of *Podocarpus* (p. 130).

The deceit can, of course, only work in nature as long as its practitioners form a minority amid really nourishing models. The same (in the opposite direction) goes for mimicry in insects. The genetic potentiality for colour in the outer layers is a prerequisite.

I do not know if passing through birds promotes germination here. In untreated seeds of *Adenanthera*, the latter process may take a year. The very hard palisade testa also fits them for life outside the rain forest. Many taxa with hard, mimetic seeds live in steppe regions. Considering the dubious gain in replacing the thin sarcotesta or aril of relatives by a thick, hard layer, just economy of materials can hardly have steered selection (cf. p. 152). Guppy (1912) criticized here "facile acceptance of adaptation", considering the event as just a utilization, as not more than the exhibition of seeds by a decaying orange. I leave it at that. The visual attraction of birds by accessory devices is present. The ancestral torsion of valves is maintained for exhibition purposes. It is obvious in *Adenanthera pavonina*, where the inner sides of the valves are yellow (see Fig. 7 and 11). In some genera the gradual transformation of juicy sarcotesta seeds into dry mimetic seeds is based on the diminishing thickness of the testa (*Paonia*, Fig. 3). Another case, already cited by Corner (1953), is *Guarea* in the Meliaceae.

I have as yet been unable to ascertain the occurrence of the type in Euphorbiaceae, but it may occur in the genera *Glochidion* and *Macaranga*, where, besides species with a coloured sarcotesta, some are mentioned as having dry, glistening, exposed seeds. A case in point may be a *Phyllanthus* (*Cicca*, *Prosurus*) species, e.g. *Ph. nobilis* (S. America) with beautiful blue seeds or kernels. Carlquist (1966) suggested deceit for some Hawaiian Rutaceae such as *Pelea*. Perhaps *Musa calosperma* (New Guinea) is a case.

Another case is found in the Liliaceae, viz. *Allium tricoccum* (Fig. 9) from North America. This species stands beside others where the testa is soft and eaten by ants, or still others where the ariloids act as elaiosomes. *Allium tricoccum* differs in having permanently attached, erect, globular, large and glistening black, but hard seeds. An investigation of the stomach contents of local birds should confirm the suspicion of deceit. The woody biotope where I found the species is rich in real berries near the ground.

Mimesis abounds in Leguminosae. In the Mimosoideae, examples are *Adenanthera* and species of *Pithecellobium*; in the Caesalpinioideae, *Batesia floribunda*, perhaps *Cassia costata*; in the Papilionideae, species of *Abrus*, *Ormosia*, *Rhynchosia* and *Erythrina*. Obviously impressed by the likeness, Ridley called the condition an imitation aril. In *Pithecellobium* s.l. some species concerned are *P. clypearia* and *P. lusorium*. The Australian species *P. hendersonii* is certainly ornithochorous, probably deceptive. See Fig. 7.

The genus *Erythrina* has many species with "coral seeds" (see p. 154). Ridley 1930 (p. 503) reported those of *E. vespertilio* as eaten by pigeons. In the steppe genus *Rhynchosia*, all seeds have the hard palisade testa typical for the subfamily, but remnants of some arilloid are present. The two-seeded pods are rarely indehiscent (then adhesive). In many dehiscent pods the torsion of the valves is weak and their seeds are rather flat, smooth and brown, marbled with black. In the section *Phaseoloides* we meet mimetic bluishblack seeds, sometimes (in *Rh. phaseoloides* and the probably conspecific *Rh. pyramidalis* in South America) conspicuously red and black. They resemble those of *Abrus precatorius* but with reversion of the colour distribution, viz. with the red part near the hilum. The section *Cyanospermum* has a further refinement for ornithochory, viz. the persistence and possibly even postfloral enlargement of the corolla or at least parts thereof (the standard). In the dry petals the red colour becomes even more pronounced than it is during anthesis, when the red is present only in the standard or as stripes on a yellow background. Buchwald (1895) pointed to the gaudiness of the pods, which look like three-coloured flowers in the African species *Rh. tomentosa*, *Rh. cyanospermum* and *Rh. calycina*. I was able to investigate in greater detail *Rh. mannii* (see Fig. 8) and *Rh. pycnostachya*, where the torsion of the valves is so pronounced that the globular blue seeds are turned outwards in prominent fashion, one by each valve, so that they contrast with the peculiar silvery, light-green tinge of the valves (here exposing their exterior sides) as well as with the stone-red, dry corolla. The seeds are dark brown but with a superficial blue sheen that gives a watery impression. The persistence of the corolla is not strictly confined to ornithochorous species but seems to be exploited there more specifically. I found this condition also (although the corolla is less obvious in this case) in a strophiolate species, *Rh. acuminatissima*, which has been placed in a different section (see p. 154).

The specific names occurring in such groups, "cantharospermum" and "scarabaeoides", refer to the likeness of the seeds to beetles. In old works this likeness has been considered as mimetic too – for insectivorous birds. The case mentioned in Ridley (p. 441) is suggestive. In the stomach of an exclusively insectivorous bulbul numerous black seeds of a vetch-like plant were found. For *Calendula* see p. 98. For *Rhynchosia* this possibility deserves investigation, though myrmecochory is more probable when the strophiole proves to be an elaiosome and the seeds are detached early (cf. p. 141). Berg (1975) reported that two species from Australia are indeed ant-dispersed. *Eriosema* may join in.

Some Cyperaceae show botanical mimesis de novo, not on a sarcotesta basis but as a progression from the inconspicuous ornithochory in *Carex* (p. 33). It concerns, moreover, fruits or even fruits surrounded by an extra bract. The tropical and less aquatic genus *Gahnia* relies on "intentional" consumption by birds other than ducks, as its fruitlets are conspicuous by their colour and by an exposed, often dangling, position outside the dark fruiting complexes. Benl (1937) described how the loosened fruitlets are kept attached to the outside in four different ways, demonstrating the ecological importance of this condition. Often the fruitlets are glistening red, orange or yellow. I include them here under mimesis because the



very hard envelope must prevent digestion of the inner parts, because the fruits do attract fructivorous birds, and because *G. mannii* even has the typical red plus black coloration. The only instance of *Gahnia* fruits found inside a bird (see Ridley and Benl) refers to *Pycnonotus bimaclatus*, a mainly frugivorous bulbul feeding on berries in Javanese mountains. The fruits were found in the stomach together with seeds of a *Vaccinium*. The bird also collects the small drupes of *Myrica javanica* (4 mm), and probably the sympatric fleshy, red pseudocarps (utricles) of *Carex baccans*, with which type *Gahnia* fruits may be confused. The originally reduced fruits of such Cyperaceae repeat secondarily (just as do those of the *Siparuna*, discussed on p. 140) diverse adaptations of real seeds, including arils. Aril imitation can be observed in the genus *Scleria* (section *Scleria*) by means of their "hypogynous disk". Ridley (see his Pl. XV) mentions the fruit of a *Scleria* sp. as having been found inside birds. In another section the disk is corky. Perhaps it is homologous with the elaiosome of some *Carex* spp.

## F. Mammals and Mammaliochory

### 1. General

The phenomenon of dispersal by mammals is best developed or preserved in tropical regions. The diaspores show essentially the same characteristics as those connected naturally with birds, and the two phenomena of bird- and mammal-mediated dispersal show a parallel differentiation in methods. Many fruits are eaten by both birds and mammals.

The above-mentioned differentiation shows a larger share of epi-(exo-) zoochores, treated separately in section K. This is connected with the rougher fur of mammals and their life on the ground. The differentiation in the structure of the endozoochorous diaspores is more pronounced, in agreement with the strong diversity in mammals.

The influence of seed-eaters has (just as in the birds mentioned on p. 29) two aspects. They can be considered as predators, comparable to pathogens and herbivorous insects. This aspect prevails in studies on the population biology of plants. We pursue the positive aspect.

### 2. Dyszoochory and Rodents

Dyszoochory is frequent when animals digest the diaspores. Rodents like squirrels, rats and hamsters destroy the diaspores of oaks, pines and cereals. They are considered to be especially harmful in American desertlike regions, although after rains seeds always germinate, having apparently escaped the onslaught in great number. Burrowing rodents may, however (like the *Spalax* described on p. 14), dig up and transport underground diaspores, and all may abandon or cache diaspores underground. In the Orient *Gerbillus* spp. do so. This is comparable to the synzoochory described for nut-collecting birds. The kangaroo-rats (*Dipodomys*) in America store desert seeds. When doing this with *Prosopis* they

contribute to reforestation, or (from the viewpoint of grazing for cattle) to deterioration. I have to quote repeatedly Ridley's observations on squirrels eating *Quercus* and *Castanea* in tropical Asia, where the cups help in transport and the spines on the cupules cause the squirrels to transport the entire spikes to a quiet spot where parts are dropped. Squirrels do store fruits in caches there (McClure, 1966). I also refer to Ridley's data (p. 380) on American squirrels storing large, wingless seeds of *Pinus* and thus acting as planters in the neighbourhood. He may be right in assuming that the hard, waxy ariloids of the leguminous plant *Sindora* and of *Neesia* (Malvaceae) are especially attractive to rodents (cf. p. 81). Tropical porcupines may be purely destructive, but many tropical squirrels (like some tropical pigeons) are more specifically fruiteaters, digesting primarily the fleshy parts. They disperse the hard drupes of *Canarium*, *Elaeocarpus* and the like over a small distance in the forest. This also holds true for *Theobroma cacao*, of which rodents eat the sarcotesta-pulp around the seeds, and for the sarcotesta seeds of some species of *Nephelium*, *Baccaurea*, and *Calamus*, of which the fruits also possess hard skins and lack the smell of typical mammal-fruits. Sernander (1927) called this way of dispersal "glirochory" (glires=rodents). The inconspicuous fruits of rattans (*Calamus*), of spp. of *Canarium* and *Elaeocarpus*, are also consumed by birds.

Burkart (1943) quoted data on the chinchilla, which can only exist in the wild where *Balsamodendron brevifolium* (Leguminosae) grows. It stores and eats the fruits (algarobillas). The important contribution of Huber (1910) contains the solution of the riddle as to how *Bertholletia excelsa*, the Brazil nut, is dispersed and regenerates in nature. Its woody capsules with internal ariloid pulp around the seeds can be opened by man only with the aid of an axe. Large rodents (agoutis, *Dasyprocta*) can open them, eat the pulp and bury the seeds as a reserve. Some *Lecythis* species there and some palms (such as *Attalea funifera*) have the same bond with these animals.

The diaspores can be large as the transport is stomatochorous (in the mouth). The large rodents discussed collect fallen fruits only (Smythe, 1970). The dropping is often characteristic. They have no counterpart in the Old World. The co-evolution of *Pinus* and squirrels involving regulation of the destructive aspect is discussed by Smith (1970).

### 3. Accidental Endozoochory

Browsing animals can swallow diaspores together with the foliage and partly evacuate them intact. In ruminants, this dispersal can hardly be separated from directed, intentional gathering of adapted diaspores. Many investigations have concerned the diaspores in the dung of vegetarian mammals, including hares. They were often carried out to explain the mass-infestation with weeds after dunging. *Amaranthaceae*, *Chenopodiaceae*, *Ranunculus*, *Urtica*, many grasses, and also leguminous herbs (like *Trifolium* species) with small pods and hard seeds can withstand digestion to some extent. For percentages of survival I refer to Ridley (pp. 336–341) and the tables in Müller (1955, pp. 88–92). This is not

the occasion to discuss in detail the agricultural effect, but one archaeological effect may be mentioned. Seeds of *Chenopodium album* were found in prehistoric dwellings in such masses that some investigators considered it to be an ancient food plant. Müller (1959) made it clear that the layers found consisted of animal dung.

We also pass over here the effect which passing through animals has on germination; later on, we shall see that seedling development is often accelerated. Many agriculturalists prefer such "animal-treated" seed for sowing. In South Africa, eating of leguminous pods by antelopes has been seen not only to produce faster germination but also to prevent or stop attack by insects, which damage uneaten seeds for the larger part. Perhaps digestion eliminates mainly the seeds already damaged on the tree, also killing the larvae inside. Janzen (1969 b, 1970) found a large difference in infection by Bruchids between seeds on the ground and in droppings, as well as between seeds underneath the mother plant and those transported some distance from it. *Acacia tortilis* was found germinating only in the droppings of elephants and impala, in E. Africa. Hastening of germination is important in arid regions.

#### 4. Adaptive Endozoochory

Mimetic deceit (which, in the case of mammals, would have to be by means of smell) cannot be expected. The rest of the chapter can, therefore, be devoted to the intentional intake of diaspores by various mammals, all with different ethology. The general syndrome of diaspores adapted to dispersal by mammals has much in common with that of ornithochores, mentioned before. In some points it deviates, according to the different ethology and sense physiology of the agents. Mammals have a sense of smell, possess teeth, masticate much better, are mostly larger, rarely lead an arboreal life, and are mostly night-feeders that are colour blind. The corresponding differential characteristics of diaspores eaten by mammals are: possession of a hard skin, which offers no impediment; a more evident protection of the seed proper against mechanical destruction, the protection often being assisted or replaced by the presence in the seed of toxic or bitter substances; a smell favourable for attraction; non-essentiality of colour; large size in a number of cases. Just as in earlier reptile-fruits, the demands of accessibility are more stringent than in bird-fruits, and dropping may be continued. For a good relation with flying mammals (bats), special requirements are evident, as will be shown later. This syndrome again represents a maximum. It is, just as in ecological flower classes, partly positive (attracting legitimate visitors) and partly negative (excluding others).

Repellent substances also often occur in the parts to be digested, as long as these are immature. They may even be toxic, as in the oily aril of *Blighia sapida* (Sapindaceae), causing the akee-disease in Jamaica. The toxic substances in seeds can also (and this is obvious in dry leguminous seeds) have the function of a repellent for seed-destroying insects (Janzen, 1969 b). Mammalian dispersal has the disadvantage of seeds remaining lumped in coherent feces.

In Northern regions so few original mammalian dispersers survive, and so many edible fruits are introductions, that it is difficult to reconstruct the original relations. The influence of ungulates on fruits remained small after glaciation, when grass was present in sufficient quantities. In fruitless periods, migration or a switch in menu was not as easy as it was for birds. Fruit-bats stayed away entirely after glaciation, as did flower-birds. Some rodents managed to survive in the habitat or reconquered it by storing dry diaspores of the advancing plants. The natural role of martens, jackals and hedgehogs has largely to be surmised. In North America coyotes play a role, even for *Washingtonia* palms. Wild boars represent the villains of the piece, although in South America the peccary is beneficial to the low-growing, fragrant ananas. We have to speculate on the inclusion in our classification system, as mammal-fruits, of the following items: medlars (*Mespilus*), melons, peaches, apples, pears, prunes, cucumbers, etc. — fruits which have, moreover, been grossly modified by cultivation. The sweet-smelling green quince (*Cydonia*) is a typical mammal-fruit. Bears had and have a modest role as eaters of berries, also as consumers of larger fruits.

The tropics offer a rich and permanent table for fructivores such as monkeys, civet cats, bats, ungulates, bears, etc. The fruits and the animals reflect each other's characteristics there. In contrast to other handbooks (Europe-centered), the one by Ulbrich (1928) tries to bring this out for tropical fruits.

**Ungulates.** Tropical ruminants and elephants eat all kinds of vegetable matter that agree with their taste. Elephants mix fruit in their herbage and in Africa even follow the fruiting of preferred trees, e.g. *Dumoria heckeli*, with large seeds. The tree is said to be distributed along the trails. The very large kernels (13 cm) of the palm *Borassus flabellifer* have also been found sprouting in the dung, together with those of *Hyphaene* and *Adansonia* and the many leguminous pods discussed below. For details see Philipps (1926), Burt (1929) and Guillaumet (1967). In Asia, *Durio* and *Mangifera* seeds have been found sprouting in the dung.

Ruminants in African savannah regions rely to a considerable extent on fruits. Antelopes can digest rather woody fruits such as those of *Adansonia*. Leistner (1967) gives some details on their specific behaviour. The springbok (*Antidorcas*) is a grazer and browser, the gemsbok (*Oryx*) and the eland (*Taurotragus*) eat more fruit. Gwynne and Bell (1968) pointed to the Thomson gazelle (*Gazella*) as a fruit-eater, in contrast to the gnu (*Connochaetes*) and the topi (*Damaliscus*). Many Leguminosae, especially *Acacia* species, specialize in this way of dispersal, offering leathery, nutritive pods, sometimes keeping them on the tree, but mostly dropping them immediately at maturity. The fruits are often classified incorrectly as dry. They are rich in protein and digestible carbohydrates, providing this, moreover, at a time when little grass is available. Nevertheless cattle breeders consider *Acacia* species in pastures as woody weeds. In contrast to dehiscent *Acacia* pods, which are really dry, the ruminant-dispersed pods spread a distinct smell, are even selected according to smell by cattle. In accordance with animal colour blindness visual attraction is absent. Another spe-



cial adaptive point is the extreme hardness of the smooth seeds, resistant to strong molars, as is evident in *Tamarindus*, *Dichrostachys*, *Acacia* and those *Cassia* species with hard, indehiscent pods of the type of *C. fistula*. *Acacia arabica* and *A. horrida* are mentioned as pioneers in grassland, spread by ruminants (also goats). Some of those trees, including species of *Prosopis*, *Ceratonia*, and *Samanea*, are even cultivated for their fruits in diverse parts of the world; in South America, they are used as cattle fodder under the general name of algarroba (properly *Ceratonia*). In North America, *Lespedeza stricta* (Papilionideae) was spread by cattle in this way. Indian deer and goats also eat large fallen fruits, disgorging the hard parts during rumination (Troup, 1921).

**Bats and Chiropterochory.** The writer has published a monograph on the subject (1957 b), of which the following is an abstract. In tropical Asia and Africa, the old group of Macrochiroptera (fundamentally fruit-eaters) has a large influence. In America, fruit-eaters developed later independently and incompletely among Microchiroptera in some of the Phyllostomidae, viz. separately in the subfamilies Stenoderminae, Phyllonycterinae and Glossophaginae.

We shall treat the pronounced cases. Many fruits are eaten by bats, monkeys and birds, e.g. small figs and *Cecropia* fruits. The bat smell of guava (*Psidium*) does not repel ruminants, that also disperse the seed.

As experience with expatriate fruits teaches, the attractiveness of bat-fruits is international, obviously depending on some general preference in bats. The taste and consistency can vary between hard-sour and soft-sweet, but otherwise a syndrome of general characteristics can easily be recognized, in accordance with the ethology and sense physiology of the bats. Fruit-bats are nocturnal and colour blind, have a keen sense of smell, and have, apparently, an innate preference for "stale", musty odours like the one their own glands produce. Flying foxes are fond of fermenting bleeding sap. The odorous components have, perhaps, not only a function of attractive signals, but also supply specific nutrients. Captive fruit-bats, fed exclusively on peeled, non-rotting fruits, including many non-chiropterochorous ones, developed symptoms of deficiency. Rarely (in the case of small-seeded *Ficus* and *Piper* species) do they ingest seeds or kernels, mostly consuming just the juice after intense chewing. After transport to a suitable place, the remnants are dropped or spat out, sometimes at the roosting places. The dispersal distance in Java for fruits in the mouth rarely exceeded 200 m (maybe more in S. America, where fruit-bats are sometimes "trap-liners" and sometimes can pick up fruits from the ground). *Artibeus* transported *Andira* over 270 m. Some S. American bats possess echo location. The larger species (*Pteropus*) can transport heavy mangoes, but other species have lower limits for loads. Fruit-bats have particular difficulty in flying through dense foliage, as their sonar-apparatus is weakly developed, at least in Old World, non-cave-dwelling species.

We have few data about the range reached by intestinal transport. Seeds of *Cecropia* and *Piper* spp. are found at longer distances in intestines and feces of Phyllostomidae. Bats contribute to figs in new Krakatoa. Osmaston (1965) re-

**Table 1.** Comparative syndrome of chiropterochory

Fruit-bats	Bat-fruits
Nocturnal visits	Exposed position, rarely nocturnal odour
vision limited, colour-blind	drab colour, rarely whitish
Good sense of smell, with preference for fermentation odour	Musty, sourish, rancid odour
Rather large	Diaspore may be large
Blunt molars press out juice; gut simple, short, providing low body weight	Weakly protected, juicy diaspore, juice easily digested
Seeds and pulp mostly expectorated	Hard parts may be large
Weak sonar system, visit impracticable inside foliage	Diaspore exposed outside dense crown (flagelli-, caulicarp)

ported seeds of *Ficus* and *Chlorophora* in droppings many miles from the trees. See also Huber (1910).

The fruit-syndrome is, accordingly (see Table 1): drab colour, musty odour reminding one of fermentation and rancid substances (butyric acid), possibly large size with possession of large seeds, permanent attachment with exposure outside the foliage. The latter position can (as in bat-flowers, described in Faegri and van der Pijl, 1979) be realized by a curious reorganization of the tree-structure, resulting in, e.g. an open structure of the canopy (pagoda structure, as in *Terminalia catappa*), projecting stalks, long stalks hanging underneath the canopy (flagellicarpy), or placement on the main trunk (caulicarp, as in species of *Lansium*, *Ficus* and *Artocarpus*).

The occurrence of fleshy fruits with a caulicarpous position struck many early observers in the tropics. This was explained by them in many ways, none of which can be accepted, though excessive weight may be involved in some cases. Archaic basicaulicarp (see p.27) may be basic in some instances. A connection with bats for either pollination or dispersal (including weight) is further a satisfactory explanation. Entire reorganization of the crown of the female trees is conspicuous in the bat-dispersed species *Chlorophora excelsa* (Moraceae), as described by Eggeling (1955) and Osmaston (1965). A possible relation between darkness and odour production should be studied.

The absence of cauliflory in tropical but bat-less Hawaii is instructive. Though cauliflorous cacao-fruits are attacked by bats, they are not as such dispersed by them. For the sake of the pulpate seeds they have to be opened forcibly, by diverse animals.

A long list of cases of chiropterochory can be found in my paper (1957 b) and a few in Kuhlmann and Kühn (1947). Some cases deserve comment here from the viewpoint of human consumption. In contrast to temperate table fruits, those in the tropics rarely (*Capsicum*) represent gaudy ornithochores, being instead mostly large and drab with a smell to which one has to become accustomed. In-

stances are species of *Artocarpus*, *Achras* and *Psidium* and wild types of *Mangifera*.

Another link with man is that "ghost trees" in international folklore are visited at night by crying bats; their visits serve either pollination or seed dispersal. Ayensu (1974) described how bats dispersed the introduced neem trees (*Azadirachta indica*) over wide areas in Ghana.

The families most popular with the bats are: Palmae (including the date palm) in which caulicarp is organizational, Moraceae (including *Antiaris toxicaria* and many *Ficus* species), Chrysobalanaceae, Annonaceae, Sapotaceae, Anacardiaceae. The first indication was given by Huber (1910). The few caulicarpous Leguminosae (among others, species of *Cordyla*, *Cynometra*, *Detarium*, *Incarpus* and *Angylocalyx*) are mostly chiropterochorous. *Andira inermis* (see Janzen et al., 1976) is even called "morceguiera" in Brazil and "andira" is an Indian native name for bat. The sole caulicarpous plant of temperate Europe (*Ceratonia*) is natural on the northern limit of African fruit-bats; its fruits, containing butyric acid, are eaten by them in time of need. In case of need, bats switch to leaves and to bird-fruits.

With regard to the evolutionary development among the flowering plants, the following can be stated: bat-fruits appear already in some Ranales, are dominant in caulicarpous and flagellicarpous *Ficus* species (including the sycomore perhaps determining in Africa the northern limit of fruit-bats), and also occur in advanced groups on one level with and alternating with ornithochorous and other fruits. In the Bignoniaceae, bat-flowers seem primary, probably having induced



Fig. 12. Mango fruits (*Mangifera indica*) dangling by weight underneath the foliage

(by the development of a special position and special odoriferous substances) the incidental switch to bat-fruits. The reverse may have happened elsewhere.

We can also review the evolution with regard to complexity of diaspores. Bat dispersal of nude seeds has been found in the gymnosperm *Cycas rumphii*, where it is not typical and is thus possibly a regressive overlapping. In *Cephalotaxus* the aromatic, pineapple-like fragrance of the seed may also indicate reptile connections, especially in those cases where it is dropped. In the leguminous plant *Swartzia prouacensis*, the seed itself, still in the arilloid phase of exposed seeds, has developed a bond with bats, whereas other species employing the same device are ornithochorous. Its chiropterochorous adaptations consist of a fairly large seed, a drab white arilloid, a brown pod and a most curious funicle of up to 3 m length, so that we may speak of flagellispermy (see Fig. 13). The smell and the occurrence of bat visits to it deserve investigation in Guyana. The same ap-



**Fig. 13.** *Swartzia prouacensis*. Dehiscent valves of pod with seed taken out, the funicle still showing its folded condition inside the pod. Herbarium specimen attached with tape. (Photo Natan)



plies to the long-funicled seeds of *Lecythis usitata* that are, indeed, collected by bats. For the arillate but short-funicled *Lecythis zabucajo* (sapucaya nut), the picking out of the seeds from the hard fruit-boxes and their dispersal by bats have been described by Greenhall (1965). He records that the odour of the aril-oid suggests that its tissue is rotting. Some *Inga* species will probably have to be included, standing at the point of divergence from reptiles towards birds and bats. Closed sarcotesta fruits (*Lansium*, *Baccaurea*) are as frequent in the list as higher pericarp fruits.

Regarding plant geography, I pointed (1957b) to the concurrence of the limits of certain plants (such as *Spondias dulcis*) with those of fruit-bats in the Pacific, reflecting, perhaps, ancient land connections, as only *Pteropus*, the flying fox, can fly tens of kilometers. Bats contributed to the recolonization of Krakatau (Docters van Leeuwen, 1936). In Australia, *Pteropus* has recently spread southwards, outside the tropics, following fruit cultivation but switching to new, unadapted species of plants.

It is synecologically important that some fruit-bats, especially in Africa, migrate to neighbouring regions with a different crop. A number of more or less simultaneously fruiting species can therefore form one food association, as well as a number of subsequently fruiting species in one and the same community where bats can have a permanent base. The latter situation has been shown to exist also for flower-bats (Faegri and van der Pijl, 1979). For the combination with sea-dispersal to islands see p.97.

Some plant species are bound to bats in a double sense, for pollination and dispersal; e.g. the wild bananas and *Sonneratia alba*. The hanging position is favourable to both processes. Simmonds (1959) reported that dense stands of *Musa* seedlings may be the result of the presence of a bat-colony in a tree.

**Primates.** Monkeys and apes are latecomers, taking advantage of ecological opportunities that open up incidentally, and forming incidental connections. They are mostly destructive, eating everything edible, ripe or unripe, also seeds and leaves, soft- or hard-skinned fruits; they may or may not be instrumental in dispersal. They are not colour blind and as arboreal creatures became less olfactorial. They rely more on visual perception than other mammals do. Some externally hard or repellent and indehiscent fruits with internal, soft ariloids, suit fruit-eaters better than they do birds. The wild mangosteens (*Garcinia*) possessing such a structure are indeed eaten by monkeys. In a cultivated form, they are eaten by man as the monkey's successor in invading the environment. Because of the absence of a bat-smell, they are even popular with newly arrived Europeans. *Mammea* is somewhat of an American counterpart. Gottsberger (1978) reported that South American monkeys open the giant pods of a *Cassia* (from the inundation forest, *C. leiandra*) for the pulpa. Many fruits of Euphorbiaceae, Sapindaceae, Rubiaceae (*Gardenia*) Loganiaceae (*Strychnos*) and Rutaceae (*Citrus*) are of this type.

More terrestrial baboon data (also concerning *Kigelia* and *Adansonia*) can be deduced from easily found excreta. Hladik and Hladik (1967) shot arboreal

monkeys in Gabon forests and collected apparently viable diaspores from the end of their colons. Details of the structure of the named fruits are not given. Many of the seeds germinated later (in France), in some cases better than untreated control seeds of the species. The same was found with baboons.

The most curious fruit of this ecological group (armoured fruits) is the large, spiny durian (*Durio zibethinus*). Its internal arilloid is preferred above everything else in Indonesia by orang utans, rhinos, tapirs, Bears, elephants and man as successors to reptiles (see p.26). The opening of fallen fruits requires skill and force. The smell is overwhelming, but not of the bat-type. Mechanically, the seeds are unprotected, but on the other hand they are toxic when raw. Even elephants defecate them undamaged. The arillode contains oil so that even panthers join in the battle for the fruit. Smaller-fruited sister species are ornithochorous (with dehiscing and coloured fruit), demonstrating the divergence from the reptile phase.

**Various Mammals.** Stopp (1958 b) discussed the geocarpy of *Cucumis humifructus*, apparently occurring together with other cases of geocarpy in desertlike regions in Africa. The position has, however, not the character of atelochory, as in the cases described in Chapter VI (see p. 2.), and the fruit is large and juicy. Stopp doubted the dispersal by aardvarks (*Orycteropus*), near whose tunnels the plants are found. Meeuse (1958) brought good arguments in support of the idea that the animal eats the fruit for its water and buries its dung with the seeds near its nest. Otherwise the seeds germinate badly.

The role of tapirs in Amazonia is discussed in the works of Huber (1910) and Kuhlmann (1947). To mention a curious case reported, they bury seeds of *Araucaria angustifolia*, so that thickets of it arise on the spot.

Such caching has, besides the lack of pioneering to new sites, the disadvantage of clustering (also exposing seedlings to grazers), thus annihilating the breaking-up of many-seeded fruits. The latter holds also for the general cohesiveness of mammalian faeces. Fallen fruits, however, are not spilt, though not only primates and bats but also other mammals are more arboreal in the tropics than in temperate forests, even at night time.

Civet cats (*Paradoxurus*) in Indonesia also consume all kinds of fruit mainly at night. They have the pleasant habit of defecating on fixed open spots, so that I could review the complete yearly menu. The data are lost, but the curious impression remains that such a small animal is able to eat the large palm fruits of *Arenga saccharifera* and defecate the large kernels. The animals can climb trees. Bartels (1964) published a list of seeds dispersed by *Paradoxurus hermaphroditus* in Java. Coyotes are of some importance in North America.

I pointed out for *Durio* that large carnivores consider its oily fruit just as attractive as herbivores do (compare carnivorous birds and the fruits of the oil palm, *Elaeis*). Another oily fruit, the avocado (*Persea gratissima*), is sought after by wild cats and jaguars in America after being dropped. The seeds are too large to pass through birds.

We badly need information on the relationship between diaspores and kangaroos (including frugivorous tree-kangaroos) in Australia. The absence of

ruminants may give an interesting background to the form of *Acacia* fruits there, as it does to the relative scarceness of spiny plants on this continent. Do cassowaries and emus (cf. p.35) fill the niche?

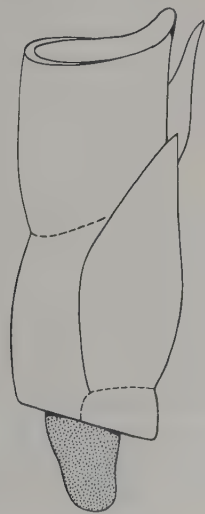
## G. Ants and Myrmecochory

Though ants are no longer considered as latecomers in history (social ants became known from the upper Cretaceous) they do not play a fundamental role; the adaptations to them in diaspores have been built on top of, and utilize, older structures. Sernander (1906) and Berg (1954) proved that their temperate cases were of preglacial origin, but pointed also to the importance of ant dispersal for late speciation. On the other hand, ants evoke to an amazing degree responses and reorganizations in diaspores, often with such a strong and fast transference of function that closely related species use different organs for attracting ants.

An old objection to the concept that selective forces in the environment are creative is that ecological selections follow physiological causation. One might first ask whether the origin of a mutation is physiological causation and further what an induced physiological modification can offer to selections. The genetic steering by selection is causal to physiology.

The older literature has been covered in review by Uphof (1942). This shows the paucity of relations between plant diaspores and the (much older) termites, which are obviously purely destructive.

One group of ants, composed of the Mediterranean and North American harvester ants (*Messor*, *Atta*, *Tetramorium* and *Pheidole*), is also dyszoochorous. They carry the most varied materials to the nest, sort them out, store the edible parts and consume these after fermentation. The dispersal effect is small, perhaps



**Fig. 14.** Diaspore of the grass *Rottboelia exaltata* consisting of two spikelets on one internodium of the spike. Elaiosome from the medulla dotted

of some importance in seeds rejected near the nest or dropped during displacement of nest sites (see Ridley, p. 523).

Experiments with truly myrmecochorous seeds are necessary to study their resistance to harvester ants. Few are found in the "granaries". Bullock (1974) gave an answer: Californian harvester ants transport appendaged seeds of *Dendromecon* and *Datura*, eat the elaiosomes and reject the seeds proper – apparently well-protected. Such ants too may show a preference for seeds with elaiosomes (Berg, 1975). Smooth spherical seeds are difficult to collect.

Among really dispersing vegetarian ants, diverse genera sometimes collect unspecialized berries but mainly specialized diaspores, eating the (mostly white) edible part, the so-called elaiosome (oil body). This soft part got its name because it usually contains drops of an oily substance. The rest of the diaspore, often hard and smooth and apparently difficult to destroy, is buried in nest tunnels or in fissures. Bresinsky (1963) demonstrated that broadly inserted elaiosomes are separated from the seed proper by special tissues, thick-walled and containing crystals. One might remark that the distance of transport is small, but more than just transport is involved; there is often also fixation in a suitable spot, thus precision dispersal. Reduction in the number of seeds produced by the plant is a consequence. Quick burial may also reduce destruction by seed-eaters (mice, granivorous birds).

It seems reasonable to suppose that root parasites can profit from burial by ants as providing early subterranean contact of dependent seedlings with host-roots. Some holoparasites are indeed myrmecochorous (spp. of *Mystroptalon*, *Cytinus* and also *Lathraea squamaria*). Even some hemiparasites join in, a few spp. of *Melampyrum* and *Pedicularis* and perhaps all spp. of *Thesium* (a Santalaceae with the flowerstalk as an elaiosome). The great majority of holo- and hemiparasites, however, possess other ways of dispersal. Other *Lathraea* spp. are ballists with large seed.

The myrmecochory of *Tozzia* mentioned by Ulbrich (1928) has to be annulled since Weber (1973) showed that the illustration of the seed reposes on confusion with *Viola*. *Allium ursinum* has to be struck off the list of myrmecochores.

In simple cases, the fleshy testa itself contains edible material in a diffuse form. This "Puschkinia type" embraces, among others, *Cyclamen* and *Ornithogalum* species. Diffuse drops of oil are present also in the seed coat of some ant epiphytes such as *Myrmecodia*, but in some of them the connection is still more vague, as just an adhering piece of the infructescence suffices (*Procris laevigata* in Java).

In most cases, a specialized elaiosome is present. My experience in Java is that the ants in question react to it like lightning; elsewhere they may act with more hesitation. At an early date, I began to doubt that oil could be the attractive factor – this on the basis of experiments with just oil. Some volatile component must be present, probably in the oil, and is rapidly perceived. The lipid often impregnates the tender outer cell walls. Bresinsky determined that the attractant is an unsaturated free fatty acid, absent in nonmyrmecochorous appendages of the seed and not always connected with visible oil drops (as in *Melica glumes*). It



is probably ricinolic acid with an oxy group which, in pure form also, attracts ants strongly, although its volatility is not great. It leads to the consumption of the inner protein, lipoid, starch and vitamins (B<sub>1</sub> and C were found by Bresinsky; these vitamins also occur in the ant-bodies of myrmecotrophic plants).

Speta (1973) studied endopolyploidy in many elaiosomes including the primitive oil epidermis of *Puschkinia*.

Sernander's large monograph (1906) on European examples led to the distinction of several types of ant diaspores, often fruits. I shall not sum them up, as Ridley and Uphof did, because ever more types are found in temperate regions as well as in the tropics. Here are some more European examples of seeds, in which a caruncle is often the basis of the elaiosome: *Helleborus* species, *Scilla bifolia*, *Galanthus nivalis*, *Chelidonium majus*, and species of *Euphorbia*, *Moehringia*, *Ulex*, *Viola*, *Primula*, *Sarothamnus*. In *Hepatica triloba* and species of *Melica*, *Carex*, *Anemone*, *Ranunculus* and *Lamium*, fruits are involved as a late convergence.

Most of the plants mentioned belong to the herbaceous spring flora in northern forests. Many occur also in drier Mediterranean regions (see Speta, 1973) (*Allium*, *Reseda*, *Hermodyctylus* spp.). There *Centaurea* spp. and other Compositae developed new elaiosomes at the base of the fruit, a process accompanied by loss of the pappus. The more tropical instances which I shall mention do not grow in dense forest; this is true even for a few of the ant epiphytes.

The refinement of the appeal to ants (looking for mere physiological causation leaves us in the dark) is demonstrated by cases where an elaiosome is formed from very special organs. In *Primula acaulis* and some species of *Melampyrum* and *Veronica*, it arises from a swelling of the funicle; in *Pedicularis sylvatica* from a protruding endosperm-haustorium (Berg, 1954). Bresinsky described the precise ontogeny of many elaiosomes, finding in species of *Melampyrum* and *Lathraea* that they arise from a separate part of the endosperm. In American *Nemophila* species, the elaiosome is the "cucullus" known for many Hydrophyllaceae. This is the outer layer of the testa with large, living and densely filled cells, a layer which becomes detached and is sloughed off by the placenta. Bresinsky diagnosed changes in dispersal, also into myrmecochory, as important factors in speciation, demonstrated especially for *Anchuseae*. On the other hand Valentine (1966) pointed out that in *Primula* species that are not closely related, convergent myrmecochory can mask the essential differences.

What interests us here especially is that specific modifications of the plant as a whole occur, bringing the seeds into the life-sphere of the ants, perhaps also protecting the tender elaiosomes against desiccation and loss of volatile components by delay in shedding. Sometimes it is rapid disintegration of the spike (in grasses), sometimes disintegration of the fruit into irregular fragments (some Hydrophyllaceae, some species of *Trillium*, *Asarum europaeum* and *Datura fastuosa*). Often the modification consists of early detachment of the seeds or the wilting of non-sclerenchymatous flower (fruit) stalks (curiously even in *Carex pedunculata*), the presence of turned-down capsules (*Cyclamen*, *Scoliopus*), acaully, or even reorganization of the flowering axis, as described for species of

the myrmecochore *Roscoea*. Nordhagen (1932) has described this process for the latter genus, a member of the Zingiberaceae from the Himalayas. Like Sernander, he and Berg (1958, 1959) pointed to such changes in dispersal as influencing the plant as early as the flowering phase, and even as necessitating adjustment for pollination (see p. 18).

When no special presentation occurs, the offering of postfloral nectar (*Melampyrum pratense*) or extrafloral nectar (*Turnera*, perhaps *Centaurea*) has been suggested to lead the ants up to the diaspores. Sernander accepted this for some myrmecochorous Labiatae but not for other cases. Explosion often (pre-existent in *Euphorbia*) cares for speedy presentation preventing the drying-up that would annul attractivity. Such diplochory acts here as a compensation for the presence of an ill-suited position. The same combination occurs in *Viola* spp., as described again by Culver and Beattie (1978).

Berg (1958) has studied some American examples in this respect, adding in 1966 a review of other cases of myrmecochory known there, for example, *Uvularia grandiflora*, *Sanguinaria canadensis* and *Asarum canadense*. In the true pericarp berries of liliaceous *Trillium* species, he found a retrograde changeover to the sarcotesta as an elaiosome. The berries were suite to birds, but the sustained pulpiness of the seeds allowed them to form elaiosomes as well. I refer to this, as an analogy to the forest plants mentioned for Europe, because the change to myrmecochory in certain species was accompanied by a change in habitat; viz. from open field to forest. Berg proposed a revised taxonomy of the genus [later also of *Scoliopus* and other relatives of *Paris* and still later (1969) of *Dicentra*] on the basis of dispersal ecology. A reminder of what has been happening in the plant kingdom through the ages!

Crosby (in Hawkes, 1966) found a reproductive disadvantage in the myrmecochorous primrose (*Primula acaulis* or *P. veris acaulis*), which seeds in woody areas. He compared it to the non-myrmecochorous erect cowslip (*P. veris* or *P. veris officinalis* or *P. officinalis*), which grows in pastures and seems purely a wind-ballist. The precision of ant dispersal was nullified by poor establishment of the seedlings. We might remark that the latter factor is usually not considered under reproductive capacity, and might also ask whether he investigated each species in its optimal habitat, also in regard to ants. Later, Berg (1966) added for California *Dendromecon*, the tree-poppy. This is interesting as it concerns a tree-like shrub and a chaparral plant. Usually elaiosomes dry out quickly in a dry atmosphere. The transference of function to a different organ, mentioned in the beginning, is clear in the myrmecochorous pairs of relatives: *Corydalis-Fumaria* and *Pedicularis-Melampyrum*. In this light even apparently equal elaiosomes in related species may have arisen independently in an archaic group, out of a common sarcotesta. This is clear in the many myrmecochorous Liliaceae, where the adaptation started with an oily sarcotesta (see p. 56). In other species it specialized into elaiosomes, in *Scilla* of raphal or exostomal origin (Speta, 1971). All this may be brought in against an assumption of Berg (1972). He found elaiosomes on two, now widely separated, Berberidaceae and assumed that this was due to worldwide dispersal by ants.

For further connections of ants with transformed sarcotesta seeds see p. 143.

In the tropics scattered cases have been found, which in this textbook will be dealt with collectively since they were often published in poorly accessible sources (cf. van der Pijl, 1955 b). Berries of *Asparagus asparagoides* are comparable to those of *Trillium*. Many grasses in dry regions have a disintegrating spike with a part of the medulla adhering to the units as an elaiosome (see *Rottboelia* in Fig. 14). Other examples include *Lochnera rosea*, *Cleome ciliata*, *Sterculia alexandri*, *Endonema retzioides*, *Desmodium gyroides*, *Cyanastrum cardifolium*, *Turnera ulmifolia*, *Datura fastuosa*, *Talinum* and *Coluria* spp., *Mystroptalon* (a parasite infecting its host underground). In some of these, parts of the placenta adhere as an elaiosome, in *Clerodendrum incisum* a placental part of the pericarp, usually serving for ornithochory in the genus. In *Curculigo orchioidea* (Liliaceae) this remains on the top (morphological basis) of the hard funicle, persisting on the seed. *Sebastiana* in Argentina is tree-like, with the combination of an explosive mechanism and the euphorbiaceous caruncle as elaiosome. Some Cyclanthaceae (*Ludovia*, *Cyclanthus*) may also be suspected of being myrmecochorous, and among the Papilionideae and Euphorbiaceae there are many representatives with beetle-like seeds (see p.44) (e.g. *Acalypha*, also in many Cactaceae, including *Blossfeldia*).

Recently Berg (1975) added some 1500 species in 24 families from Australia, partly based on actual observation. Like *Sebastiana* they differ from N. European forms in being not mesophytic forest plants but xeric shrubs. Their firmer elaiosomes and the lack of subsidiary presentation devices may be connected with the habitat or explosive presentation. A few diaspores collected are drupe-like, without a distinct elaiosome. The relation seems to have been developed here de novo.

For a more experimental approach to the dynamics of myrmecochory see Culver and Beattie (1978).

A special group of myrmecochores is formed by the ant-epiphytes of the tropics. They live in the carton "ant gardens" on trees or provide nesting places themselves in hollows. Ule (1905) described the situation for Amazonia. Some of those Araceae and Bromeliaceae there, though specific for ant-nests, have weakly myrmecochorous, berry-like fruits. In Java, Docters van Leeuwen (1929) found true myrmecochory in those ant-epiphytes [species of *Hoya* (see Fig. 15), *Dischidia*, *Aeschynanthus*] which have oil in primarily anemochorous seed-hairs; also there live in the nests some orchids with oil drops in the testa. The seeds are larger than normal, not anemochorous. No wonder that some are also brought to the nests inside *Myrmecodia* tubers. The famous "living ant nests" of *Myrmecodia* have (as said before) near ant dispersal (although distant ornithochory is more important) and offer postfloral nectar to their inhabitants. Docters van Leeuwen found that even some hollow-stemmed inhabited ferns had switched to myrmecochory by the formation of oil drops in the sporangium walls – unchanged through aeons, but now modified under the influence of ants.

When speaking about ants in general it is necessary, even when one leaves pure carnivores aside, to point out that finer specificity exists, especially in guests



**Fig. 15.** Ant garden of a *Crematogaster* sp. in Java with plant and seedlings of *Hoya lacunosa*

of ant-epiphytes. Janzen (1974a) paid some attention to this side and to the nutritive role of ants living inside domatia of some ant epiphytes.

## H. Wind and Anemochory

### 1. General

Aerobiology and its methods will not be discussed here. Though it concerns spore dispersal, one book may be mentioned for a mathematical treatment of transport distances and deposition possibilities in dust diaspores (Gregory, 1973).

It has already been mentioned (p.22) that anemochory, although extensive, is not basic in seed plants. It may be important for the distances reached, but is less efficient than animal dispersal where the chance to reach a comparable, suitable



habitat is larger (see pp.29, 31, 33, 62 etc.). Its preponderance in certain regions reflects the climate and the biotic poverty and is, essentially, a feature of a pioneer vegetation. Müller (1955) cites data for the alpine flora (60% anemochorous) and the Mediterranean garigue (50%). For other floras, I refer to Chapter VI C. The influence of climate need not be a direct one. Open regions provide vegetative opportunity for grasses and these can be largely anemochorous.

In anemochory we can distinguish plain horizontal displacement of the air, dynamic and thermal turbulence, both culminating in cyclones, and a simple slowing down of falling diaspores by air resistance. The propelling effect of the latter on winglike structures provides time for sideways displacement.

Botanical engineers are able to work out the dynamics and the quantitative side of fall velocity. Dinger (1889) and Schmidt (1918) compared different structures as to their possibilities and formulated technical calculations for theoretical cases. Schmidt calculated for many species the average limits of dispersal, the distance which 1/100 of the diaspores can reach. Assuming an average turbulence of the air of  $A=20$  (g. cm. sec.) and a wind velocity of 10 m/sec, he found for the spores of *Lycoperdon* and *Polytrichum* respectively 470,000 and 19,000 km, for the diaspores of *Taraxacum officinale*, *Picea abies*, *Pinus sylvestris* and *Fraxinus excelsior* respectively 10, 0.3, 0.5 and 0.02 km. The double distance can seldom be exceeded. With the same wind velocity, dispersal limits for other diaspores can be calculated by means of the equation  $V_g : x = (S_x) : (S_b)$ . In this  $V_g$  is the known limit of a known diaspore,  $x$  the one to be determined,  $S_x$  the fall velocity of the latter and  $S_b$  the fall velocity of the known diaspore.

When a diaspore becomes detached at a higher wind velocity only (a factor of ecological importance), the distance increases with the square.

Feekes (1936) checked for some anemochores in a newly drained open polder some formulae of Schmidt for absolute distances and fall velocities, not to be reproduced here. His results in the field agreed with expectations and showed some limitation for the distance reached, for instance 5 km in *Aster tripolium*. He admitted that incidental plus variants may obtain higher results, a fact which is also ecologically important for pioneering.

Müller (1955), from whom the foregoing is partly derived, gives tables of various aerodynamical data. The dynamics are interesting in the special group of the wind-ballists, intermediate between anemochory and autochory.

The difference in methods of anemochory makes presentation of a general syndrome (outside enlargement of surface, relative to weight) impossible. The factor of exposure is also important. The negative influence of humidity on wind dispersal requires auxiliary mechanisms for exposure at the right time. This serves to compensate for the indiscriminate nature of the vector. This is evident in pappose Compositae when the involucre releases the fruits only under certain conditions. Sheldon and Burrows (1973) studied this and the effect of a dry atmosphere on the pulvini of the pappus bristles, serving to spread them outward. Opening in dry air only (xerochasy) is apparent in anemochorous

species of *Pinus*, but not in other species. The opposite effect, viz. opening after wetting (hygrochasy), is important in some desert plants, where rain is beneficial.

In grasses, anemophilous and anemochorous exposure at the end of culms coincide. The relation to open plains is evident. In other cases, dispersal requires its own structures for exposure, for example, in some low-growing orchids where extreme elongation of the pedicel occurs after anthesis. In many epiphytic orchids, exposure of the seeds to the wind is brought about by elater-like hygroscopic hairs from the placenta that gradually push the seeds out of the fruit (see Fig. 17). Ulbrich (1928) considers this as just a loosening up, but I found real ejection in *Taeniophyllum*. In *Dendrobium crumenatum*, I found that the seeds in the baccate but dehiscent fruit appear as lumps of twisted seeds. The seeds themselves untwist with lively movements when drying.

As to the distances reached, Ridley (pp. 3–10) gives some values for distances covered during storms, which I shall not repeat. Müller (1955) presents some verified data for such situations (recorded in kilometers): *Abies* 7, *Pinus sylvestris* 2, *Betula* 1.6, *Acer* 4, *Fraxinus excelsior* 1/2. Others have found: *Tussilago* 14, *Populus* 30, *Senecio congestus* 200. Wolfenbarger's (1959) confused paper is full of data on everything living. The extremes given do count, even though the dilution effect should not be neglected. Heintze (1932) gives (pp. 155–216) many data on the effect of cyclones. When worms, stones and fishes are transported, why not seeds (cf. Hedberg, p. 91)? The rather large seeds picked up by planes at high altitudes testify to apparently improbable possibilities.

On the other hand, a stay in the cold upper air with strong radiation may kill many seeds, as is assumed in particular for orchids, which show little dispersion over tropical oceanic islands. Though in this case mycorrhiza and pollinator specificity may be complications, there exist other cases of plants with dust-seeds that nevertheless cover only limited areas. This has been cited as proof that anemochory is not an important factor in their distribution.

Too distant a dispersal of single diaspores brings problems with establishment of the species. Some orchid seeds from the West Indies are blown to Florida, where they grow into plants but cannot reproduce for lack of pollinators, as Dr. C. H. Dodson wrote me. There are other limits to extension of area by means of an anemochorous apparatus (as we shall see in our discussion of colonization and establishment on p. 108), but that Krakatau harboured anemochorous plants a few years after the eruption is a fact that cannot be reasoned away by the far-fetched objection that nobody saw the seeds fly and settle.

The origins and backgrounds of anemochory are just as manifold as they are in the anemophily of flowers, a phenomenon which also appears in a great number of zoophilous groups. In ancient Gymnosperms, anemochorous sidelines had already begun to develop. In Angiosperms the changeover may be located in the seed or in the fruit.

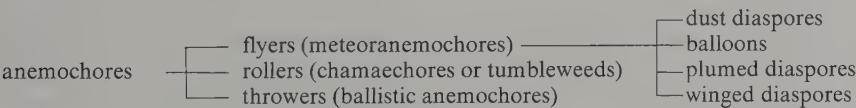
The uniformity of small anemochorous seeds in orchids goes back to ancestral terrestrial forms like *Apostasia*. The condition may be connected with mycotrophy and the ensuing diminished chance of finding a suitable substrate.

In Compositae (see p. 159), the origin is connected with the emergence of single-seeded fruits, even in high trees (*Vernonia* spp.). In primary Ranales, anemochory is practically absent; in “Amentiferae” it is scattered and has a secondary character.

We have seen that in most cases the two spheres of life, pollination (microspore dispersal) and seed dispersal, are strictly separate things that do not mix. In orchids they are even radically opposite in character. In the anemochorous Compositae, only a few have wind pollination for their flowers; in the anemophilous Cyperaceae, only a few have anemochory. In some incidentally deviating species with wind-flowers in diverse families, there is concurrence of the two spheres, as evidenced by species of *Poterium* (Rosaceae), *Thalictrum* (Ranunculaceae), *Hardwickia* (Leguminosae), and *Fraxinus* (Oleaceae). This concurrence is not so evident in incidentally deviating wind-dispersed species, indicating that the change to anemochory is obviously less profound.

Before starting a review of subclasses according to the behaviour of diaspores, it is necessary to point out that much dispersal by wind is incidental, especially during storms, and is not based on any special structure. Diaspores may cling to dead leaves or may (e.g.) be blown over plains and ice while forming part of various structures. Wind also exerts an influence on floating diaspores, so that the classification that will be given below might be complemented with “swimmers”.

The dividing up of adapted forms between subclasses serves mostly to bring some descriptive order into the manifold structures whose function is to enlarge the relative surface. The resulting classification does not have such a pronounced ecological-evolutionary character as those in the other chapters, and the same is true of the agent. I use some terms from Müller-Schneider and quote Ulbrich frequently; both authors gave a full descriptive documentation of great morphological interest.



2. Dust Diaspores

As previously stated, the apparent return to spores manifested in this group may in many cases have a relation with physiology and with the multitude of diaspores necessary for them to be omnipresent and to discover the special substrate that limits their distribution. Saprophytes, mycophytes and ordinary parasites are dominant in the list of families with sporelike diaspores: Orchidaceae, Pyrolaceae, Orobanchaceae, Scrophulariaceae, Balanophoraceae, Burmanniaceae, Sarraceniaceae, Droseraceae, Nepenthaceae. Weights for some species from the first three families were given as 0.003, 0.004 and 0.001 mg respectively.

We find very small seeds also in other groups, e.g. in some Crassulaceae, Caryophyllaceae (*Gypsophila*, *Sagina*), Campanulaceae, *Eucalyptus* and *Rhododendron*. In some cases a link with epiphytic life is present, as it is in tropical Gesneriaceae. For a possibly supplementary function in germination of the pitted testas see p.74. Rauh et al. (1975) presented fine scanning photographs and pointed to the possible importance of preventing wetting before dispersal and (anew) for penetration.

The small, flat (scobiform) diaspores of many species are a transition to winged diaspores.

### 3. Balloons

In the already small-seeded Orchidaceae and others, the loose testa may assist in forming a balloon, but usually this feature is associated with fruits. The inflated and indehiscent pods of *Colutea arborescens* (a steppe plant) and of species of *Anthyllis* first spread over a short distance through the air, away from the mother plant, to proceed subsequently as tumbleweeds. Some *Trifolium* species have blown-up calyces or form balloon-heads by other means (see Fig. 26). There is also a transition to rollers in Polygonaceae (*Pterostegia* and *Harfordia*) by means of bracteoli, and in Chenopodiaceae from steppes with the aid of inflated bracteoli (*Atriplex vesicarium*) or perianth (*Kochia* and *Suaeda*). Some Umbelliferae from the steppes possess cavities in the pericarp (*Cachrys* and *Prengos*). Balloon fruits are known from Sapindaceae (*Cardiospermum*), Rosaceae (*Physocarpus*) and Scrophulariaceae (*Physocalyx*).

In some grasses, as well as in hops (*Humulus*), the infructescence is balloon-like, but the separate fruit-bracts are more or less flat. Some *Anemone* species have groups of plumed achenes that can adhere to form a balloon.

### 4. Plumed (Comose) Diaspores

Except for epiphytes, possession of plumed seeds or fruits is again rare in forests, frequent in open vegetations. In seeds a simple start on this way is elongation into one long hair (*Trichosporum*). Seeds of *Lephaimos* (a saprophytic member of the Gentianaceae) produce one hair from the long funicle and another one in the opposite position by elongation of the integument. In Asclepiadaceae and Apocynaceae, a tuft apparently arises from a split-up wing, as it may also in some Malvales. In Bromeliaceae (*Tillandsia*), the tuft is of intricate origin, perhaps (as in other cases) derived from an arilloid. The hairs of *Salix* and *Populus* are outgrowths of the placenta, even arising in close association with unfertilized ovules.

Seed-hairs may sometimes serve the purpose of enlarging the surface for hydrochory (see p.73). Some plumed seeds float regularly on the tuft (*Bombax manguba*) and are then eaten by fish in Amazonia. For *Typha* see p.77. The ecology of the seed-wool of *Gossypium* and *Ochroma* needs investigation in order to answer the question as to whether it is more significant for wind or for water



dispersal. Stephens (1966) performed experiments on buoyancy and salt tolerance, which proved that the wild *G. darwinii* may have reached the Galapagos Islands by sea, but that this is not certain for cotton species on more remote Pacific islands. According to the ideas of Janzen the hairs may also function to keep off the bugs which are so fatal to malvaceous seeds.

In some waterside *Rumex* spp. (*R. hydrolapathum*) wings serve as sails on floating diaspores.

In fruits, a simple solution is the persistence of the style(s) which eventually bear hairs (diverse Ranunculaceae, some Rosaceae such as species of *Geum* and *Dryas*). Steppe grasses (such as *Stipa* and *Aristida*) develop long, hairy awns, which may possess collateral functions such as boring and attachment to animals. Even pods of Leguminosae may develop anemochorous plumes (*Adesmia*). The calyx-pappus of Compositae, particularly, may show hygroscopic movement, which has the function of regulating the moment of dispersal. Curiously, a number of Composites (among others *Lasiospermum*) abolish the pappus and develop achenes that are hairy all over. The hygroscopic bristles on *Clematis* plumes may also assist in the drilling in of fruits. In an apparently fine pappus functional reduction can occur when the plumes break off easily (*Cirsium* spp.). The famous diaspores of *Leucadendron* (Proteaceae) consist of the fruit, dangling beneath the four persistent, feathery sepals.

Sheldon (1974) pointed out that a pappus may function (cf. Gramineae) to keep the water absorbing scar near the soil.

## 5. Winged Diaspores

Flat wings provide the means for gliding or, when one-sided, for dynamic propulsion. In both cases, they can function in providing lift to diaspores much heavier than those in the previous classes, but heaviness of necessity limits the distance and requires launching from a tree or a high climber.

First, seeds. The most famous, giant seed-wings (15 cm and very light) are found in *Macrozania macrocarpa*, a cucurbitaceous climber in tropical forests. One may doubt the effectiveness within the forest, but Ridley cites arrival on a ship at sea. High up in the canopy there may be turbulence. Many Bignoniaceae have large, winged seeds, for example *Oroxylum indicum* in Malaysian light forest and *Pithecoctenium* in tropical America.

The wing of many Abietinae is a detached part of the fruiting scales, not part of the seed. Data concerning the ordinary "range" of the seeds (40–800 m) are known, but exceptional longer travel distances are important. In some Sterculiaceae (*Pterygota*), the wing is clearly a transformation of an arilloid testa. Its vascularization is a physiological regulation of the kind mentioned on p. 17. (It is present in the outer integument of (also winged) seeds of *Lunaria*, but not in other Cruciferae (Bouman, 1975).) This transformation is also apparent in other arillate groups with incidental wings (Meliaceae, Bombacaceae and Celastraceae such as *Lophopetalum*), and in some African leguminous high trees belonging to the Piptadenieae. In some cases the wing is a lateral expansion of the funicle or a

web between its loops (some Hippocrateaceae, Ixonanthaceae, Proteaceae). Winged fruits are very effective in the cases of *Alnus* and *Betula* spp., where they are small.

The one-winged propelling type is called a samara, best known from *Acer*. Its aerodynamics and a comparison with the construction of an airplane wing need not be discussed here. The type occurs in a wide range of families, including the Leguminosae. The wing is apical in *Pterolobium* and basal in *Myroxylon* (reversed samara). In *Centrolobium robustum* (Brazil) the wing is 17 cm long. Many *Pterocarpus* and *Dalbergia* species have a circular wing around the pod. In *Erythrina lithosperma*, the pod dehisces and each valve with adhering seeds forms a samara, once found at some kilometers from an isolated tree. *Daniellia* (tropical Africa) has a queer fruit with the separated endocarp rolled up and the seed dangling underneath. It is said to rotate during wind dispersal, but I have my doubts as it stays too long on the tree and as the funicle top forms a small arilloid. Even in Magnoliaceae, carpids can become dry samaras (*Liriodendron*). In some Compositae (*Dahlia*, *Moschardia*) inner chaffs connected with achenes provide samaras. In samaras two types have been distinguished: one rolling with a high terminal velocity, the other non-rolling with a low one (Green, 1980).

Some fruits develop several wings on their sides, which again results in the production of rotating diaspores. Very impressive are those of *Cavanillesia* (Bombacaceae), high Amazonian trees, where the wings are up to 9 cm wide. The type also occurs in *Piscidia* (Leguminosae) and even in low-growing Polygonaceae (*Rheum* and *Rumex* species).

Such side wings are often formed by accessory parts contributed by the flower. In *Triplaris surinamensis*, the originally white wings from the perianth crown the fruit as in a shuttlecock. The accessory wing of *Tilia* is formed from a bract, those of *Petrea volubilis* from the calyx and those of *Congea velutina* from bracts. In the latter two, well known in tropical gardens, the coloured wings first collaborate in attracting animals for pollination. Among Labiatae, where the persistent calyx often assists in dispersal, we find in *Ballota acetabularia* a detachable calyx with the apical part as a flat wing. The whole resembles the diaspores of Dipsacaceae, Compositae and certain *Trifolium* species.

The function of the calyx wings of Dipterocarpaceae in South Asian forests has long been under discussion. The weight of the diaspores (up to 30 g) and general experience are objections to the acceptance of common anemochory in the forest which, in addition, is rather windless in its lower regions. Ridley found them usually no more than 10 m away from the mother trunk, rarely 30 m. The incidental aggregation in pure stands is perhaps a consequence. Seeds from more isolated trees of a *Shorea* species were, after a storm, found to have covered 400 meters, but these seeds do not germinate in the open. Like Ridley, Heintze (1932/35 on pp. 186–194) has collected quite a literature on the subject. It has been assumed that the wings, after the fruit has fallen, can provide the special position required for germination, but this has also been denied. Later research offered nothing new but a novel view described on p. 75. The non-dormant fruits can be decimated locally by swine and rodents, though less frequently than in *S.*

America. Their gregarious fruiting (or cued mass flowering) is often considered as providing satiation to predators. One asks whether exhaustion (as after a mast-year of acorns) is not a sufficient, physiological explanation.

The wings on the fruits of *Begonia* and *Dioscorea* species and in the inflorescences of trees of *Hymenodictyon* (S. Asia) have no direct dispersal effect, as these fruits are not detached and not one-seeded. They may help the wind in shaking the fruit, an activity needed for the liberation of the small anemochorous seeds. Presentation merges into dispersal, as is also the case elsewhere. In the case of *Tilia* there exists doubt about the generally accepted anemochorous function of the large bract on the infructescence. It may just shake the fruits loose as a transition to ballistic anemochory (Jones, 1968). Perhaps it served before, in pollination, for heightening visibility for moths. For transition to ballism see p.69.

### 6. Tumbleweeds

A transitional group is formed by light diaspores with enlarged surfaces that neither glide nor fly, but are blown over the soil (eolic drift). Winged diaspores of many *Chenopodiaceae* from deserts belong here. Their appendages have also some significance for fixation and germination. Scientific terms for the process of dispersal through tumbling are chamae-(anemo) chory ("chamai"=on the ground) and anemogeochory. Especially here, the diaspores may consist of large parts of plants or even whole individuals that are or become globular. In



Fig. 16. Infructescences of *Spinifex squarrosus* on a shore in Java

windswept steppe regions tumbleweeds are frequent, and travellers there have described how their dwellings were overrun by masses of rolling plant material.

The special modifications are the curling up of flat parts and detachment devices of those parts or plants. The reversal of the hygroscopic curling up after moistening, so well known for the "Rose of Jericho", can result in anchoring by flattening in a favourable spot, accompanied by liberation of seeds. This famous name refers to *Anastatica hierochuntia* (Cruciferae) of the Near East and North Africa. Because of its opening and closing branch system, the whole dead plant is sold by florists, but other plants (*Selaginella* species) are often substituted for it in the trade, as is the Composite *Odontospermum pygmaea*.

Already in 1887, Volkens denied the old story of the rolling of *Anastatica* and Stopp (1958b) complained that the plant only rolls in the literature (even in Ridley and Ulbrich), since in reality the taproot is too tough to break off, so that the uncurling is only the hygrochastic presentation device after rain so common in semidesert plants. Other local observers, however, have confirmed the rolling away and the accumulation of the plants in depressions, stating that the tough taproot has no laterals and can sometimes be torn out by the wind. Another plant from dry Mediterranean regions also has the reputation of a roller; viz. *Plantago cretica*. Zohary (1927) denies this, admitting only the curling up and uncurling of the fruiting axes as in *Anastatica*. The same rash generalization has been made in herbaria for inflated pods of *Crotalaria*, which are not detached at all. Other inflated pods (of *Colutea*), as discussed under balloons, do finally detach and roll. Nordhagen (1936a) reports that even some dehiscent pods of northern *Astragalus* species can roll away; such pods possess devices for keeping the seeds in place during the process. Some *Medicago* pods, spirialized into smooth balls, may also be rollers, although most are hooked and epizoochorous.

*Physalis* species with their light, inflated calyces are not simple rollers, either. The enclosed fruit is ornithochorous and detachment is doubtful, so that at best diplochory may be assumed. The related genus *Przewalskia* has fruit-calyces that are more likely to act as tumblers, and the same holds for some species of

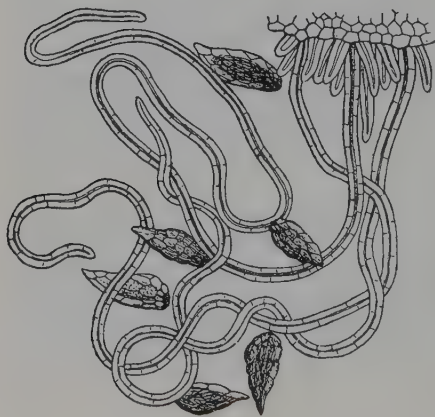


Fig. 17. *Anguloa roezli*. Seeds with elaters from the placenta. (After Velenovsky)



*Hibiscus* and *Pavonia* from African steppes with inflated, globular calyces (Ulbrich). In the Mediterranean region, the curious *Fedia cornucopiae* (Valerianaceae), to be discussed later (p.99), has globular infructescences that break off easily and roll. In the thistle-like Composite *Gundelia tournefortii* of the same region, the whole plant behaves in this fashion; so do the American plants *Psoralea argyrophylla* and *Atriplex canescens*, which have abscission joints at the base. North America has many more tumbleweeds in some Amaranthaceae and Chenopodiaceae (*Cycloma*) and in the introduced species *Salsola kali*. Zohary (1937) listed many cases from Palestine, most from the less arid regions. On Indonesian shores and in Australian plains, the round infructescences of the grass *Spinifex* (see Fig. 16) are known as "windballs". The shore species *S. littoreus* (*squarrosus*) also endures sea transport (like *Salsola kali*). It has to be analyzed, case for case, whether the whole complexes stay together (synaptospermy) until a favourable spot is reached or whether parts or loose diaspores are shed during the voyage. Feekes (1936) reported the latter for rolling complexes of *Suaeda maritima* and Chenopodiaceae in a new open polder, leaving long lines of seedlings afterwards, just as Monod (1974) reported for Saharan *Schouwia* (*Iberis*) *thebaica*. The balls of *Spinifex*, however, are few-seeded and seem to be buried whole.

In some species of *Stipa* the long awns can secondarily form globes by intertwining.

Unspecialized small diaspores, mixed with organic fragments, can be blown over open surfaces (eolic drift). Russian botanists have suggested that the flora of Nova Zembla has arrived there from the continent in post-glacial times, blown over ice.

It seems unnecessary to translate and introduce the many terms of Huth, Ulbrich and Heintze for all kinds of rolling and flying anemochores or those for anemochores that are incidentally moved over snow fields.

## 7. Wind-Ballists (Anemoballists)

The subject of wind-ballists is rather neglected in current handbooks, though its mechanics are clearly a coordinated system of specialization in structures (Berg, 1969).

It concerns plants with jacitation, a throwing mechanism which is put into action by wind, in contrast to autonomous ballists and those that are worked by rain or by passing animals (see Section L on autochory).

The best-known contrivance is the "censer mechanism" of *Papaver*, by which the long, elastic pedicles swing to and fro in strong winds and the capsules broadcast the seeds (through apical pores) over quite a distance. For *P. somniferum*, Ulbrich has measured distances of up to 15 m. The seeds are much heavier than those in censers constructed just for exposure to wind. The rattling septa of *Lunaria* (Cruciferae) are capable of throwing the heavy seeds that are not detached with the valves. Many Campanulaceae are comparable and also have pores at the top of erect capsules and at the base of hanging ones,

preventing the seeds from simply falling out. A parallel censer (with additional xerochasy) is made by a Hawaiian tree lobelia by queer transformation of a berry (Carlquist, 1965). As its seeds are anemochorous, this censer approaches the case of *Begonia* (p. 67). The names *Trematocarpus* (or *Trematolobelia*) are fitting. The same jacitation occurs in many Caryophyllaceae and species of *Scrophularia* and *Antirrhinum*, and perhaps in *Primula veris*.

According to Müller-Schneider, the long, tough peduncle of *Bellis perennis*, helped by the postfloral shape of the torus, can throw out the pappusless achenes when swinging. Granivorous birds, muddy feet and rain transport them farther away.

## J. Water and Hydrochory

### 1. General

According to Heintze (p. 18), the term "hydatochory" of Ulbrich and followers goes back to a slip of the pen of Engler.

Water plays a limited role in the dispersal of land plants and an important one for plants of swamps and shores, although the relation is far from general, as many "sea grasses", Juncaceae and Cyperaceae rely on animals (ducks, fishes) - and on wind. In these cases the agent provides directed dispersal to the right substrate. In Cyperaceae (see the index) the means of dispersal are very varied. Chermeson (1924) has analyzed the background of hydrochory in 30 species.

In some cases the seeds sink but the liberated seedling can help out by floating for short-range dispersal.

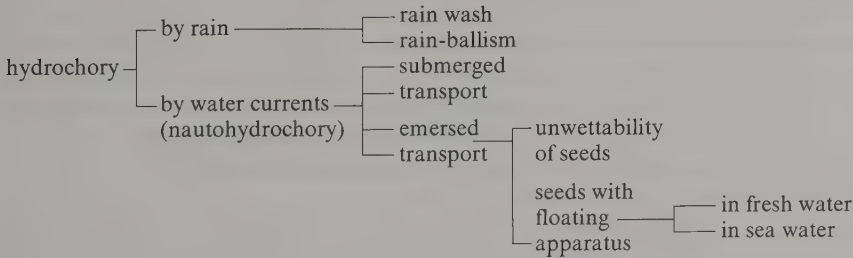
Quite a number of aquatics (including spp. of *Callitriche*, *Butomus*, *Hippuris*, *Myriophyllum*) show no hydrochorous adaptations in their diaspores. These may rely on smallness of transport on muddy feet (Fauth, 1903). For the anatomy of floating devices I refer to the literature of Müller, 1955, 1977.

When present, the connection with water is clearly utilization, derived from all other possible conditions. It is practically absent in Gymnosperms (for the case of *Cycas* see p.97). Even in families around Hydrocharitaceae, basically returned to water life, the general hydrochory is of a secondary nature (see p.73). In *Limnocharis* the folliculate mericarps float briefly, their open suture then widens and liberates the (sinking) seeds. In more derived *Alisma* spp. the fruitlets are one-seeded and float on the indehiscent pericarp, which surrounds a reduced testa. This reduction in seed numbers occurs in many aquatics. Ancestral dehiscence is disturbed. In hyphydrophiles such reduction can also be ascribed to poor chances of pollination. Aquatics in general stick to old modes for pollination, but methods of dispersal seem to change more easily. The number of aquatic plants which make use of water for dispersal is much larger than the number that pollinate by means of water.

The still more aquatic family of the Podostemaceae has also maintained insect pollination (and seed-setting) in the air, both processes taking place when

the water is low in the dry season. Willis (see Ridley) reports for Ceylon that the seeds of *Lawia* become mucilaginous when wetted and may stick to the feet of birds walking over the rocks. In Venezuelan species of *Rhyncholaxis* and *Mourera*, Gessner and Hammer (1962) saw very fast mucilage formation; they think that this serves the purpose of anchoring seeds to rocks, a process which in this case is demonstrably effective even in running water. An objection to direct water dispersal is that at this period the water level is said to be far below the level where the plants are ultimately found attached, which is the highest level ever reached by the water. Accorsi (1953) interprets the situation for some species (of *Apinagia*, *Mourera*, *Meniopsis* and *Tristicha*) as merely a new establishment on the same spot by the mucilage, atelechory in a dangerous environment. He observed germination to take place mostly at the beginning of the rainy period in or on the open fruit, from which the seedlings fall on the rock, subsequently to be attached by hapters. The place of attachment was below flood level. Grubert (1974) found, in the field, that only anemochory is important for upstream dispersal.

Because of their secondary, incidental and convergent character, it is difficult to describe concisely the structural modifications of hydrochory. We have already seen that they are often based on anemochory. Though the chance of arrival in a favourable location is generally larger in hydrochory, the two have in common a connection with an abiotic, wasteful and unselective agent, working with weight and surface area. Hydrochory shows a diversification paralleling that of anemochory; the submerged diaspores can be compared with flyers, and the floating ones with rollers, while ballistic hydrochores also exist. However, the subdivision of the class adopted here has to pay some attention to the special nature of water as an agent. The presentation of the diaspores is also comparable. Many hydrochores bend their fruit stalks down (*Cabomba*, *Victoria*, Hydrocharitaceae), whereas in *Nuphar* (not purely hydrochorous) the seeds mature above water. The following scheme presents a functional review.



2. Rain Wash (Ombrohydrochory)

In this group (“ombros”=rain) we find unspecialized plants owing their dispersal to rain, which flushes the diaspores away over some distance. The phenomenon has rarely been analyzed and cannot explain the appearance in new habitats, especially when going uphill. Ridley (p. 165) observed it in the rain

forest and in botanical gardens for small, low-growing plants with diaspores too heavy for wind dispersal. Mountain streams can complete the action, carrying the diaspores to unusually low, temporary habitats.

The exposure to rain is often promoted by hygrochasy, the opening of containers in a humid atmosphere. Many swamp plants also rely on this opening mechanism for floating seeds (*Caltha*, *Veronica* spp.). Curiously, the phenomenon has some limited importance for short-range dispersal in arid regions with occasional showers. There, some open leguminous pods ("Rinnenhülle") as well as the fruits of *Sedum acre* and of some Mesembryanthemaceae open in rain and let the seeds go without further devices (see p. 101).

Zohary (1937) reports that the cruciferous fruit of *Leptaleum filifolium* also opens at well-defined times as a "Rinnenhülle" (fruit with open groove). It is uncertain whether the rare rains have a dispersal effect in some desert Compositae such as *Geigeria acaulis*, described by Stopp (1958b). The dry involucre is folded over the fruiting heads until rain comes. The Rose of Jericho perhaps also belongs here (see p.68). Investigators in North American deserts ascribe dispersal over farther distances to rain floods over hard-baked surfaces (Spalding, 1909). Monod (1974a, b) mentions cases from the Sahara, including *Indigofera oblongifolia*, *Psoralea plicata*.

### 3. Rain-Ballists

In a small group of plants we find a repetition of the splash-cup mechanism, where falling raindrops provide the energy to make diaspores jump out of cups. In Fungi and Hepaticae it is not rare. The phenomenon is found in fruits from dry regions, where showers thus provide both dispersal and the possibility of germination.

Müller (1955) separated the group from Kerner's old group of general ballists. In the newly created category, raindrops make a lever mechanism swing back and throw the seeds out of containers. The capsules of *Eranthis hiemalis* and horizontally oriented pods of some species of *Iberis* and *Thlaspi* (Cruciferae) catch the impact of raindrops well. For *T. perfoliatum*, Müller mentions a throw of 80 cm. In some Labiatae the throwing is said to be effected by the concave upper lip of the calyx (e.g. in some species of *Ocimum*, *Prunella* and *Scutellaria*). Brodie (1955) devoted papers to the phenomenon (of spring board mechanism). His assumption concerning *Hyptis suaveolens* does not tally with my experience (see p.78). Nordhagen (1963a, b) criticized the creation of this category (see p.86), but I could confirm experimentally Müller's observations in *Thlaspi alpestre* and *Aethionema saxatile*. In the latter the lower, winged siliculae exhibit simultaneous hygrochasy, whereas the seeds exhibit myxospermy (see p.71). For the genus *Alyssum* Zohary (1949) studied the evolution of varied dispersal methods. His application of the term "ombrochory" seems unjustified in some spp. where rain makes the enclosed seeds swell by their mucilage so that the valves open. These are not actively horizontally orientated during rain, as in spp.



like *A. damascenum*. Savile (1979) analyzed the impact of raindrops (mainly of the larger ones dripping from wet foliage) on fruits of some Saxifragaceae (*Mitella*, *Chrysosplenium*, *Tiarella*). For the latter cf. p. 87.

#### 4. Submerged Transport in Water

Many aquatic and shore plants possess diaspores that are not appreciably lighter than water, especially some marine Helobiae and species of *Callitriche*. They are nevertheless transported by currents, assisted by some enlargement of surface by means of hairs (*Peplis portula*, *Nymphoides orbiculata*). In *Nymphaea alba* and *Euryale*, the seeds even float for a shorter or longer time on a transformed ancestral ariloid. The hairs of *Limnanthemum* (*Nymphoides*) *nymphaeoides* are said to cause (see, however, p. 74) flotation as long as they are filled with air, but can also serve as hooks. In the Acanthaceae some riverside species (*Hygrophila*) have adpressed seed hairs, which are erected in water to form a slimy mass, in the Orient consumed by man (like the nutlets of *Ocimum*). This dispersal may be incidental utilization of a family character serving usually (in the many desert representatives) the myxospermy to be discussed later.

Some aquatics (*Ottelia*, *Hydrocharis*) have seeds that sink, but slowly, due to the effect of a slimy cover, developed after decay of the berry-like fruitwall. They imitate frog-spawn, which may be fortuitous. The function of the slime may be (as in *Eichhornia* and some Nymphaeaceae) to replace the lost dehiscence. The less aquatic relative, *Butomus*, still has aerial dehiscence.

Hovering diaspores are typically found buried in exposed sedimental silt, whereas floating diaspores are more typical for stable shore lines.

In this type and the following one, some atelechorous mechanisms prevent too long-lasting a displacement, just as in the case of wind-dispersed steppe plants. Usually it is the disintegration of the swimming apparatus that causes anchoring in the mud. In *Aponogeton* the testa bursts. Sometimes anchoring hooks help in final fixation and establishment; this is true also for the originally floating fruits of *Trapa natans*, the water chestnut. The hooks on the exarillate seeds of *Barclaya* (a Malaysian water lily) and perhaps some *Blyxa* spp. probably serve primarily this purpose, although they can also adhere to water-visiting animals. Ulbrich (1928) lists some water-burrs (see our Fig. 21), among others species of *Zostera* and *Ceratophyllum*. Even some vegetative, seedlike winter buds of aquatic plants (e.g. marine najadaceous *Cymodocea* (*Amphibolis*) *antarctica*) possess such anchors. They are lacking in Hydrocharitaceae and Alismataceae, but sunken seeds start with producing anchoring hairs on the hypocotyl before the root develops. The large, floating, free seedlings of *Amphibolis* (p. 118) are enclosed in a spinous structure. Recent authors (including de Cock, 1980) deny any anchoring of fruits in *Zostera marina* as the curved stigmas are shed and the fruit, though one-seeded, dehisces. This lack of anchoring (also in the seeds), explains difficulty in reseeding, and stands in contrast to the related *Phyllospadix*. When ducks or other animals contribute to dispersal this may be (? also) for the sake of the enveloping spatha. The seeds are

collected by some Indians for food, who wait until diving ducks signal their ripeness.

The seedlings of *Avicennia* possess a special anchor. Veins of the decayed perianth of *Polygonum lapathifolium* provide it (Staniforth and Cavers, 1976). Even the spores of fungi, returned to aquatic life, acquired a spiny anchor.

The sharp spines on the dehiscent fruit of *Victoria amazonica* are (like those on its leaves and stalks) purely protective (against vegetarian water animals), without significance for durinology and dispersal.

As an appendix, which might be placed anywhere in this section, I give a list of water and waterside plants dispersed (also) in the seedling phase, hovering in currents or floating on the surface: *Lythrum salicaria*, species of *Juncus*, *Hottonia*, *Sagittaria*, *Mimulus luteus*, *Primula japonica*, *Stachys palustris*, *Scrophularia aquatica*, *Aster tripolium*, *Salicornia herbacea*, *Enalus acoroides*. The cases of *Inga* and mangrove plants are dealt with elsewhere.

## 5. Floating Diaspores

The first, rather accidental, possibility for floating is that small seeds, though of high specific weight (but also anemochorous dust seeds) are unwettable and float on the surface of water, taking advantage of the surface tension. The cause of this unwettability can be the chemical constitution of the testa and the existence of small pits in it, filled with trapped air. A tropical instance is *Isotoma longiflora*. When submerged, the seeds sink. Müller-Schneider adds fruit of *Ranunculus repens*, *Myosotis scorpioides*, *Cirsium palustre*. Surface tension can also make diaspores actively spread over the surface (*Nymphaea* spp.).

Burgeff (1936) analyzed the unwettability of seeds, leading to penetration into the soil, as a supplementary function in temperate, terrestrial orchids, contrasting the situation with that of epiphytes.

The rather large seeds of *Thlaspi alpestre* (see p. 72) float for many days in pits on the surface membrane. When a detergent is added to the water, any slight disturbance makes them pierce the membrane. This change is reversible after a return to pure water. The flat, unwettable seeds of *Nymphoides* (see p. 73) can rest for a long time on the surface membrane, also by their marginal bristles. As in other such "floating" seeds agitation of the water makes them submerge (cf. Velde- Heyden, 1980).

The most frequent cause of floating is low specific weight, achieved by air spaces, lightness of albumen or cotyledons, or corky tissues. In fresh water this is sufficient equipment; protection is superfluous. Often the potentially protective layers are shed. Loss of dormancy and immediate germination occur, perhaps to be explained causally by disappearance of inhibiting factors. See the list of seedlings above.

Lotus fruits (*Nelumbo*) attain, after having been desiccated, a prolonged dormancy (of some centuries). The persisting receptacle breaks off and floats upside down. The loosened nuts sink. They emerge again, producing (at least in *N. lutea*) floating seedlings.

There is no reason to list many cases, as few principles are involved. Often the low specific weight is entirely fortuitous, as the plant has no natural relation with open water. Praeger (1913) analyzed buoyancy in British plants.

In Carices and grasses (*Glyceria*, *Coix*, *Oryza*), glumes and other bracts assist. Wind and currents help in the transport. Dispersal here is in harmony with the habitat, though many riverside plants are not entirely bound to water transport (see p.64). Among riverside species of *Sonchus*, *S. palustris* developed the best collateral floating power. As the genus is primarily anemochorous, the establishment in the specific habitat rests on factors other than dispersal. Sometimes inland races of the same species differ in buoyancy, showing the relatively recent action of selection. Ridley (p. 240) comments on the relative rarity of hydrochorous Cyperaceae (*Mariscus* and some *Cyperus* spp.). For the combination with ornithochory see p.33. *Carex* spp. are discussed by Chermezon (1924). *Alnus* spp. vary from wind to water.

The preceding discussion refers to plants connected with pools and quiet streams, not with fast-flowing rivers and torrents. In the latter the fluvial hydrochory provides only downward transport, so that upward dispersal remains a riddle and overland transport by birds must be invoked (cf. Podostemonaceae, p. 71). In this connection a warning is necessary: plant sociologists, interested in distribution, use the term "fluvial plants" in a different sense, namely for species which enter a region along river valleys or are restricted to the latter.

Flowing rivers carry much "drift" of diaspores, but this transport is mostly ineffectual, as many drift-seeds are dead or doomed to death. Guppy (1906) deals with river drift too, mentioning, e.g. *Dioclea reflexa* from river banks as spread by water, but many of the drifting seeds are already dead on reaching the sea. Stopp (1956) analyzes (with the same result) the drift of the Congo river. He refers to other cases, including the fossil seeds that trouble paleontologists as they possibly rest on secondary sites. The frequent occurrence of dry-land plants such as *Mucuna*, *Entada* and *Physostigma* spp. tallies with the results of studies on marine drift (see below). I fear that Stopp sees things too black-and-white, as some of the dead diaspores are really hydrochorous and die only after too long a stay in water, for lack of anchoring devices. Staniforth and Cavers (1976) critically analyzed the drift in a shallow river in Ontario.

In tropical forests there are species which frequent riversides, like others mentioned on p.24, but have fruits adapted to river transport: in South America, e.g. *Grias cauliflora* and species of *Combretum*, whose seeds are dead when they finally reach the sea. For Malaysia, I cite species of *Hodgsonia*, *Pangium edule*, *Gluta reinghas* and the stenophyllous (narrow-leaved) *Eugenia salicoides*. The sea-dispersed *Barringtonia* species can be seen as derived from river-dispersed species, like *B. spicata*. The same goes for *Calophyllum inophyllum* and the riverine *C. macrocarpa*. Ulbrich mentions *Fiebrigiella gracilis* from Andean river shores. *Mimosa asperata* belongs here, too. Ridley deals with this group separately on pp. 197–241, including even *Hevea brasiliensis*. Ridley (1930) (p. 202) also included riparian Dipterocarpaceae, as *D. oblongifolius*. One is inclined to suggest that the anemochorously inefficient wings (see p.66)

originated in such hydrochorous forms, where they acted for enlargement of surface or even as sails on corky, large, floating fruits (cf. *Gyrocarpus* and *Bombax munguba*).

In sea water, a much more aggressive substrate in which a much longer stay can be expected, the floating apparatus has to be more sophisticated. The dispersal mostly concerns land plants, some of which are more or less tolerant of salt. An impermeable layer protects the embryo in most cases. In the giant drupe of *Cocos nucifera*, this layer (endocarp) was present in its organizational type; the fibrous mesocarp serves for floating and the endosperm has in its "milk" a provision for establishment on a shore without much fresh water. This can be seen as a beginning of vivipary. The "nut" germinates above ground, a process promoted by rainwater penetrating into the abraded husk. A number of temperate shore plants also are dispersed by sea (*Cakile maritima*, *Crambe maritima*, *Lathyrus maritimus*), as are many halophytes from tidal mud. *Aster tripolium* has become diplochorous, being dispersed originally by wind but secondarily by the floating of achenes and seedlings. This rarely serves for long-range dispersal. The same is true even of reduced marine aquatics of the *Zostera*-type, though the seed of *Zostera* itself can endure a long stay in salt water, it does not float, but sinks soon (see p. 71).

Ridley pointed to the case of tidal *Dolichandrone spathacea* (Bignoniaceae), which conquered by its floating seeds a tremendous area compared to its anemochorous, riverine sister (or parental) species. Its more or less pantropical distribution is also connected with the substrate, which is the same over a wide region. This dispersal can overcome barriers between continents. Thorne (in Meggers et al., 1973) pictured the curious distribution of Humiriaceae, a purely American family. One species, nearly related to an American *Sac(c)oglottis* species with floating kernels, lives in coastal West African rainforest.

In the Cruciferae *Cakile* and *Crambe* the decisive properties of the diaspores seem primarily connected with a different biotope, already weakly halophilous (see p. 99). Marine *Cakile* spp. have a desert counterpart in *C. arabica*.

The tropical sea drift contains many diaspores with full vitality. The classical description is the one by Schimper (1891). Others, among them Guppy (1906), investigated for many instances the time span over which vitality is retained in sea water. The best-known seeds, washed ashore even on European beaches, are of the adventitious type, such as the hard seeds of *Entada*, *Mucuna* and *Cassia fistula*, which are found in fluvatile drift. The seeds are mostly dead, and the living ones rarely germinate or grow on the seashore. The famous *Lodoicea seychellarum* belongs in this group. The giant nuts do not float when fresh. Most of the viable drift diaspores belong to shore plants from the mangrove or *Barringtonia* formation; of the genus *Mucuna* only *M. gigantea* is represented.

We shall not discuss all details, but mention the curious seeds of *Caesalpinia (Guilandina) bonduc* and *C. bonducella* (Leguminosae). They look like pebbles, are extremely hard and can float for years, thus providing an almost pantropical distribution. For the influence of sea currents see Guppy (1917). Some indehiscent, anemochorous, winged pods of species of *Dalbergia* and some hard



joints of loment (jointed pods) of *Desmodium* species could easily change to hydrochory in shore-dwelling species. Among the Compositae, only a few have switched to sea dispersal. The best known is *Wedelia biflora*, with a corky pericarp and no pappus. In *Diotis* the persistent corolla forms a flotation organ. A peculiar case is that of *Thuarea sarmentosa*, a grass of sea sands on Pacific islands. It has one female spikelet at the base of the rachis, which folds over it, becomes thick and hard and forms a protecting and floating cover over the caryops. *Hernandia peltata*, a seashore tree, has a fleshy open cup formed by the calyx around the fruit; the latter floats on the cup, although it can also float by itself. The cup has primarily another function, as we shall see for many cases of transitional, polychorous beach plants in the section on polychory.

We may finally return to the coconut, a favourite subject in discussions on origin and dispersal. Against Ridley and others who emphasized loss of viability after a prolonged stay in salt water, but with the support of other botanists such as Hill, Bünning and Docters van Leeuwen (1936), it must be maintained that the tree is actually sea-dispersed in Indonesia and over certain Pacific islands, where it germinates and grows spontaneously as a native behind the floodline (cf. Fig. 22), but is of course lacking when the population and animals collect or destroy the nuts.

We have now met sufficient proof (already presented by Ridley, p. 250) that hydrochores, especially on the seashore, are a mixed crowd, derived from inland plants. This does not preclude the possibility that a reverse, later evolution can also have occurred, as Guppy argued. We shall find support for this idea in our discussion of island floras.

In this field we find again that dispersal is but one of the factors determining the presence of plants. In tropical salt-marshes *Pluchea indica* is wind-dispersed, apparently as ill-directed to water as the *Aster* and *Sonchus* spp. discussed above.

So is aquatic *Typha*, but its plumed fruits have a bond with water. Before liberation from the infructescence the perianth hairs prevent wetting. After that the fruits can float briefly on them, but then they dehisce hygrochastically, so that the freed seeds sink (Krattinger, 1975). For epizoochory of the pointed seeds see p.25. Many beach plants are bound to the sandy shore merely by virtue of being xerophytic plants, tolerant of salt. *Spinifex* and *Tribulus* (see p.80) are examples of this, as are the aloes and cacti found as adventives on tropical beaches. We have already discussed *Sonchus* and *Aster tripolium* on tidal flats, where *Statice* species are old immigrants from steppe regions. These forms are primarily anemochorous, already more or less halophytic.

Sometimes a frequent occurrence along (tropical) streams has no connection with dispersal or with vegetative preference. It can be due to absence of seed-predating beetles in wet habitats (*Sabal* in Florida).

## K. Epizoochory, Transport on the Outside of Animals in General

### 1. Diverse Origins

As we mentioned before, we shall discuss this class separately because here the way of transportation is more specific than the agents concerned. Epizoochory by birds has already been mentioned (p. 28) and will again come to the front in the discussion of island floras (Chapter VI).

The term exozoochory is also in use for diaspores with adhesive mechanisms (spines, hooks or viscid exudates), which detach easily from the mother plant and are mostly placed near ground level.

In seeds the phenomenon is rather rare, especially in the early phase of fruit development where the seed dominates in dispersal (*Barclaya*). In some derived Leguminosae (species of *Erythrophloeum* and *Clitoria*) the viscid exudation seems a secondary device for further transport, as in the Podostemonaceae. These instances are in some cases combined with explosion and active deposition of the seeds on passing animals; this is also true for *Ecballium*, some species of *Oxalis* (see section L on autochory).

Some endozoochorous berries are internally so slimy that parts of the contents may come to stick to the exterior of the animal (see *Viscum* on p. 29 and *Rhipsalis* on p. 109), especially when the berries finally split up, as in *Calla*. The viscid substance adhering to seeds of some water plants (*Ottelia*, *Hydrocharis*) may be primarily hydrochorous, although it may also stick to the feet of waterfowl, as mentioned before.

The intricate situation, to be analyzed functionally in each single case, is further complicated by the presence of mucilage after wetting of the seeds of non-aquatics. This mucilage functions primarily in establishment (see p. 116); but in the case of *Plantago*, *Luzula* and *Sporobolus* species it also has an effect for epizoochory. The field is full of simple utilization, in accordance with its lateness. In Labiatae the mucilaginous epidermis of the nutlets stands in general relation with germination and is generally well protected against premature wetting by hairs in the throat of the calyx and by opening of the calyx at the time of liberation only. In Java, however, I found that the calyx of *Hyptis suaveolens* is wide open at maturity, exposing the two nutlets to rain. This deviation is not incidental and accidental; the swelling causes one sticky nutlet to come out while the other remains inside, and the calyx separates easily. The reduction to two nuts is significant.

In more cases from humid regions mucilaginous, not detached, diaspores function in epizoochory, e.g. in *Boerhavia erecta* (Nyctaginaceae), a widespread tropical weed, where slime is produced, after wetting the attached anthocarps. Other spp. of the genus have sticky glands on the "fruit". Another transfer of function is found in acanthaceous *Haplanthus tentaculatus*, where the seed-coat has been digested before maturation (cf. p. 10) and the outer layer of the endosperm takes over the function of forming mucilage, present in seed-coats of relatives. Again (see p. 16) proof of the relative unimportance of histogenetical homology! See also *Oxalis* on p. 116.

In fruits of all morphological types, adhesive mechanisms are so varied that classification is meaningless. Sometimes (*Forskahlea* in African steppes) even hooked vegetative parts that can root are a means of dispersal. We may, however, point out the importance of some types and also tidy up some loose ends.

## 2. Trample Burrs

The class of "Trampelkletten" (trample burrs) of German authors, such as Ulbrich and Müller-Schneider, contains hard burrs lying on the ground. Ridley (p. 571) found it difficult to account for the transformation of pappose, wind-dispersed achenes of "normal" *Rhagadiolus* (*Hedypnois*) spp. from steppes into hooked pappus-less ones in other species. In *Rh. stellulatus* whole heads change into (trample-) burrs after the smooth inner achenes have been liberated. They



Fig. 18. *Martymia annua*. Kernels after detachment of pericarp valves

may also act as ground-rollers, as always with the side-effect of anchoring. Comparable fruiting heads that break off have been reported for *Rh. creticus* (Müller, 1955). It should be noted that the sharp rays of the "stars" are not just achenes but fruits enveloped by hard involucre bracts and thus firmly attached. Murbeck (1920) has pictured many trample burrs, including the one-seeded ones of *Onobrychis viciifolia* and other queer synaptospermous leguminous pods (*Biserrula* and *Hippocrepis*). Ascherson founded the class after Kerner reported diaspores of a *Tribulus* (puncture vine) as being present on the hoofs of sheep, even piercing them with claws sharper and harder than in ordinary burrs. Its members are frequent in steppe regions and thus occur in families specialized for this habitat: Chenopodiaceae (*Bassia*, *Spinacia*), Zygophyllaceae (*Tribulus*) and Pedaliaceae (*Josephinia*, *Harpagophytum*, *Martynia*); also in some other Leguminosae (horned species of *Astragalus*) and, of course, also in Gramineae (*Cenchrus* spp.) and Cruciferae (*Bunias*, *Lonchophora*) from arid regions. The Mediterranean *Emex spinosa* (Polygonaceae), has such burrs, partly drawn underground as a transition to geocarpy; so does *Neurada procumbens* (Rosaceae), where the hypanthium is flat, with spines on the fruiting side (Fig. 23). We meet here the double face of desert diaspores: spines for epizoochory (they were found on resting camels and were imported into Gran Canaria in this way) as well as for anchoring. I found them in *Neurada* lying almost all with the spiny side down, well anchored, as Murbeck (1919/20) pictured them. In the text he speaks in one place about anchoring, in another about the seedlings piercing the flat side with taproots when this side is pressed against the soil, as seen in Fig. 23. Others pictured the seedlings with the persisting hypanthium in this position. According to Prof. Galil (Tel Aviv) germination occurs only in this position, so that the majority described above represents those remaining ungerminated. Monod (1974a, b) found almost all the spines facing upward. In *Echinophora spinosa* (Umbelliferae) the entire umbel around the fruit (from the single central hermaphrodite flower) changes into a trample burr. I do not know if they are dropped to the ground. Stopp (1958) listed new cases of "Trittklettenpflanze" for arid South-Africa, including *Pretrea*, where the fruits are bent post-florally to the ground, where they expose two hard thorns facing upwards. In the study of 1962 on other Pedaliaceae he paid special attention to the aspect of anchoring (see p. 116) and expressed doubt concerning the burr nature of the diaspores, though others actually found them on hooves and in fur. For *Martynia* see Fig. 18.

That the fruits contain many seeds does not tally with atelechorous anchoring. It also stands in contrast to most epizoochorous diaspores, but during the transport the seeds are trampled out gradually through slits (see Ihlenfeldt and Hartmann, 1970). Dr. B. J. D. Meeuse (Seattle) found again in Arizona that dropped kernels of *Martynia proboscidea* point the horns upwards and that they were indeed caught on the gym-shoes of his students and on hooves. For Leguminosae see p.82. For the entirely comparable *Harpagophytum*, the trampling in of liberated seeds is even necessary to obtain good seedlings. That most kernels remain in situ is, of course, no counter-argument.



### 3. Water Burrs

Even some hydrochores among Pedaliaceae (*Trapella*) show claws; in *Trapa* they certainly cannot be trampled upon and clearly serve the purpose of anchoring only. Ulbrich concedes this and admits also that not all spiny fruits are adhesive, since adherence of such “water burrs” to fishes is improbable. We have already discussed this group under hydrochory. (See also Fig. 21).

### 4. Burrs and Other Adhesives Above Ground Level

Some spiny infructescences, never dislodged from the mother plant, are known as shake- or rattle-burrs (“Schüttelkletten”). They will, in this book, be dealt with in the section on autochory as a special kind of ballists. Let this be a warning not to rely for ecological conclusions on the mere presence of spines and hooks! On the other hand, non-detachment at maturity should not be prematurely assumed, as was done by Ulbrich (1928) for *Arctium* (*Lappa*). Dr. B. J. D. Meeuse (Seattle) has informed me that the burrs of *Arctium* can be detached and transported the following spring, when the seeds germinate well. The here still numerous achenes are not liberated before this time.

The American cocklebur (*Xanthium*) has an epizoochorous burr (female head only), readily passed to animals. On pp. 18, 39, 80 we already met cases where the dispersal function integrated the fruiting head into one dispersal unit. In *Xanthium* the epizoochory is connected with reduction to two achenes, in South American *Rolandra* to one – already expressed in the floral phase. So is the transformation of pappus in general. Burrs are rare in Ranales, frequent in weedy pioneers such as most of the Compositae. The adhesion in these cases is achieved by several other means besides a hooked pappus, as in *Bidens*, or a hooked involucre (*Xanthium*). *Siegesbeckia orientalis* has spread all over the tropical world by means of viscid involucre bracts. Some South American weeds of this family (*Tragoceras*) found a queer detour; the pappus vanished, but the withered corolla took over as an epizoochorous hook. In *Adenocaulon*, the achenes themselves are covered with viscid glands. All this functional convergence goes far beyond the mere “utilization” presumed by Guppy (see our p. 3).

Just as in *Echinophora*, sterile flowers of *Cyathula* (Amaranthaceae) provide the hooks of burrs. This division of labour has clearly a directed function.

In North America, *Solanum rostratum* is known as “buffalo-burr” because of the curious change of the berries of the genus into spiny burrs. The Gramineae have also produced some plants with burrs; for instance, the Australianized small-burr-grass (*Tragus racemosus*) and some species of *Cenotheca*, *Spartina* and *Echinolaena*.

In terminal, pioneering, weedy forms, the Leguminosae have developed hooked and viscid pods, sometimes jointed pods that break up easily: species of *Desmodium* (tick seed), *Medicago*, etc. When growing above ground level, these should be classed as burrs. The function of the gummy spines on pods of *Sindora*

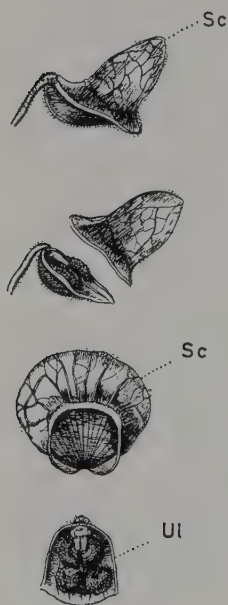
spp. (dropping from high trees) is not clear; neither is it obvious in the case of the resin in the pericarp of *Trachylobium*, although such pods (of *Colophospermum*) have been found sticking to hooves. That the somewhat comparable *Hymenaea* drops its pods at maturity may point in this direction, though they contain a sweet pulpa. The resin below the surface has also been considered as a floating device and as a deterrent to seed beetles.

The vegetative bulbils of *Remusatia vivipara*, which lives on rocks and in tree forks in tropical forests, are burrs. Otherwise burrs are rare there although some undergrowth herbs (Umbelliferae, Compositae, Gramineae) and the weed *Achyranthes aspera*, penetrating along footpaths, have adhesive diaspores. The sticky fruit of *Pisonia* trees has been discussed earlier.

Pricking into and hooking in on fur are associated with sticking on. The sharp beaks and spiny barbs on diaspores of some grasses and Cyperaceae (*Rhynchospora*) stand apart as more of a boring type, penetrating into the fur of mammals. The limits between this type, that with anemochorous awns, and the subsequently groundboring one in *Erodium* (see p. 116) are not sharply defined. Plumes adhere easily to fur and to tree bark. Many *Stipa* species use both methods of transport and some (*S. setacea*) are a pest to sheep as the spikelets even penetrate the skin.

## 5. Other Spiny Fruits

Many fruits, e.g. those of *Bixa*, *Nephelium* and *Datura*, low or high in morphology and taxonomy, fall (like the tangent-ballists to be discussed) into



**Fig. 19.** Fruiting calyx of *Scutellaria altissima*. (Sc scutellum.) The upper figures from the side before and after dehiscence, the lower figures from the front, upper and lower part separated, keeping the nutlets in place. (Nordhagen, 1936 b)

the category of acanthochores of Dansereau and Lems (1957), though the spines have no direct relation to adhesive dispersal, at the most serving as protection against being prematurely eaten. The cupule of *Castanea* and *Fagus*, not a fruit and not arillate, also belongs to this group, which seems to lie outside our field, as do the diabolical pods of *Mucuna*, with toxic, stinging hairs.

There remains, as an explanation, "archaism". Croizat explains such outgrowths as remnants of "unsexualized" scales between perianth and ovary. In inferior fruits like *Sechium* and *Victoria* this is difficult to visualize. Corner's "Durian Theory" proclaims an a-morphological archaism. The durian (*Durio zibethinus*) got its Indonesian name (the spiny thing) from the short, very hard spines on the fruit. In this case, some protective function is clear, since at maturity the spines make access to the arilloids impossible to all but the largest mammals. In the "Durian Theory", however (to be discussed on p. 139), the spininess is proclaimed to be a primitive archaism, a companion to primitive arilloids. This seems somewhat exaggerated, considering the above-mentioned spiny fruits and the fact that many really primitive fruits such as those of *Archidendron*, *Sterculia* and *Paeonia* (see p. 136) lack external spines. The only member of the Sterculiaceae I know to possess spines has late, explosive fruits. Corner (1976) sees "durianology" even behind the bristles of gooseberries.

## L. Autochory, Dispersal by the Plant Itself

### 1. General

Many authors have considered it as evident that the treatment of dispersal methods should begin with those exerted by the plant itself. They combine these in one category, that of autochory, as opposed to all other methods, which use some outside influence and are combined in the category of allochory. The term "active dispersal" is less fitting, considering the passive ballists to be discussed, in which the demarcation from allochory is not sharp and some outside influence is necessary.

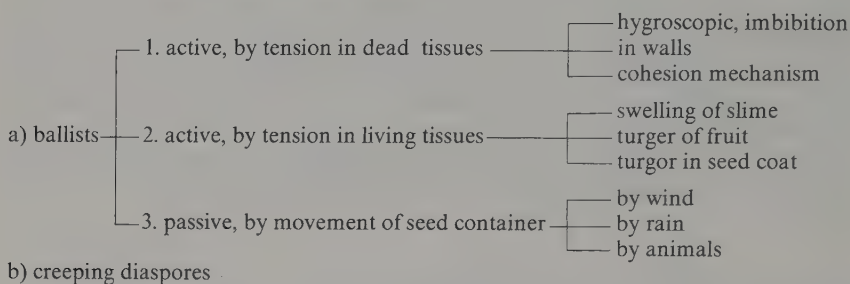
Generative diaspores can also be spread to some extent by growth alone (blastochory). This occurs, for example, when stalked inflorescences curve down for presentation, or when fruiting axes creep into fissures (*Linaria cymbalaria*), or when creeping stems drop seeds (*Polygonum aviculare*) or bury them (many geocarpous plants). Our concern is here with more active processes of autochory.

Autonomous self-dispersal is often just a further development of motions serving exposure or presentation of diaspores to some agent. We shall see this clearly in the explosion of late legumes and in some Rutaceae, where the endocarp first pushes out the seeds and in terminal cases propels them (as occurs in *Esenbeckia* and *Metrodora*, described in Kuhlmann and Kühn, 1947, in which the seeds are collected later by ground birds).

Explosive liberation of diaspores is, of course, an old feature. It is found in fungi and fern sporangia, mostly (unless it concerns large aggregates) as a

presentation to wind. It also occurs, as an escape, in spores, seedlings and bulbils of species of *Lycopodium* and *Selaginella* (see p. 127). In the flowering plants the seeding organs had to rediscover it, which happened especially in the higher families. In the Annonaceae only one instance has been described. Autochory is frequent in arid regions. The ejected diaspores are rather heavy. The opinion of Ulbrich (1928, p. 40) that ballists live mainly in woods (vide *Impatiens*) is untenable. For the mechanics of the processes see the anatomical works mentioned on p. 2.

The term "ballists" is generally used in Europe and also in the terminology of Clements (1905) and Dansereau and Lems (1957). Ridley and his followers prefer the (too vague) term "mechanical dispersal". For our "passive ballists" Clements uses the term "mortar fruits".



The foregoing survey distinguishes several methods of autochory, partly according to structural differences, partly to ecological differences.

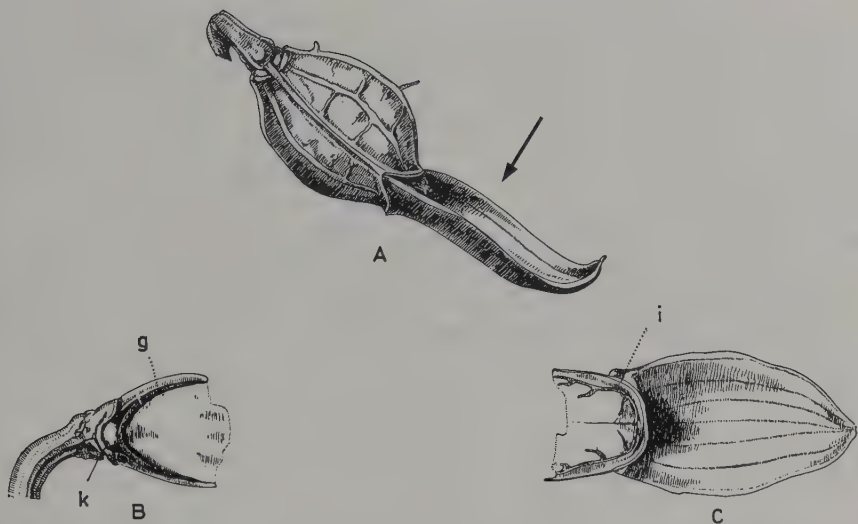
We shall discuss the effects, not the mechanisms, and shall leave open the question of whether the swelling of slime belongs to a) 1 or 2. Moreover, sometimes more than one mechanism is concerned in a movement.

## 2. Active Ballists

The term ballists ("ballo"=I throw) goes back to Kerner (1891). Later authors made subdivisions; most cases concern herbs, but trees are also included. The release of tension in dead tissues is best known from the classical legume. For a discussion of the mechanics involved here, I refer to Fahn and Zohary (1955) and earlier authors. The tropical low tree *Bauhinia purpurea* was considered as holder of the record (15 m). Müller (1955) collected a list of distances.

In the Euphorbiaceae this kind of explosion is frequent even in trees (*Hevea*), with the record of 45 m for *Hura crepitans*, the sandbox tree. The mechanisms are different in species of *Geranium* (p.p.), *Viola* (p.p.), *Buxus*, *Dictamnus* (Rutaceae), *Montia* (*Claytonia*) (Portulacaceae), *Polygonum virginianum*, *Collomia* (Polemoniaceae) and *Alstroemeria* (an exception in Monocotyledones). Some owe their wide distribution as weeds to ballism. Some show a certain rhythm over the day.





**Fig. 20.** Silique of *Carrichtera annua*. **A** The whole with the spoonlike tangent from the sterile part. **B** The springy part of the replum, still attached. **C** The tangent and part of the replum broken off at the ejaculation of the seeds. (Nordhagen, 1936 b)

Plants of the family of the Acanthaceae are said to have elastic funicles, indicated as “jaculators”. Sell (1969) demonstrated, however, that these hooks serve only to put seeds in a place favourable for ejection by the splitting valves. In many species including *Ruellia* the fruits split after wetting of a weak spot and the ejected seeds have the coat of hairs mentioned for *Hygrophila* on 73. Hygrochasy is combined with myxospermy providing rapid germination after occurrence of rain as the proper cue. In the Cruciferae the silique can eject seeds after sudden loosening of the valves, sometimes with the assistance of a sucking force in the air (Overbeck, 1925). Seeds of *Oxalis* and *Biophytum* have a turgid outer testa, which splits and ejects the rest of the seed over a distance of more than 2 m. In some Moraceae (*Dorstenia*) apparently the same thing happens, but it is the small fruit which pinches the kernel out. In the related forms *Pilea* and *Elatostema*, both Urticaceae (also forest herbs in the tropics), staminodes eject the whole, small drupe. Tension of the living fruit wall is the causative force in *Lathraea clandestina* and species of *Impatiens*. In the gourds *Elaterium* and *Cyclanthera* the endocarp and placenta, under pressure of the mesocarp, split it and uncurl suddenly, throwing the seeds out. In the squirting cucumber (*Ecballium elaterium*), the sticky pulp with the seeds is ejected by pressure. Cooperation of touching animals is sometimes needed here to release the tension and to transport seeds farther, so that the explosion has the nature of presentation. This may be valid for some ballistic, pointed utricle of *Carex* spp. and also for the small loranthaceous parasite *Korthalsiella* and also *Arceuthobium*, where the viscid kernels are liberated explosively from the fruit (Smith, 1966). The distance reached is sufficient to colonize higher branches and

neighbouring trees, but the wide distribution may be due to birds. Some species reached Hawaii. The kernels are viscid. Hinds and Hawksworth (1965) demonstrated speed and ongoing dispersal in North American woods. The distance of 400 m from the mother plant, mentioned in Ridley, may be due to secondary bird transport. We have found many more instances of secondary transport after explosion. *Viscum japonicum* has explosive fruits, Sahni (1933) saw no bird visitors.

Precision in depositing seeds on visitors joins the endozoochorous precision of members of the Loranthaceae (p.29) and is associated with the special structure of their seeds (p. 119). This hemiparasitic family is also known for the precision of some of its flowers, which throw pollen on special visitors which pinch them in the right place.

### 3. Passive Ballists

Ever since Kerner (1891), this group has often been designated as the ballists proper. The action of an outside agent does not just release internal tension, but itself provides the energy for the action. Often special structures transfer the energy in the desired way. If one considers the result only, the event may be treated also under the respective agents, as has been done here to some degree. The transferring structures are, however, too nicely convergent and too illuminating as to their function to permit omission of their curious morphology here.

First, there are wind-ballists swaying on long stalks. They have already been mentioned as ballistic anemochores on p.69, Kerner also included pappusless Compositae, such as species of *Centaurea*, in this group.

For rain-ballists see p.72.

Next come ballists operated by passing animals. Nordhagen (1936 a, 1936 b) distinguished these as "tangent-ballists" from anemochorous "holo-ballists", where the shock acts on the whole plant. Some of them have shake-burrs which do not detach, but grip passing animals and return like a spring to their former position, ejecting the diaspores. Many Labiatae have infructescences shaped like globular balls, receiving shocks on protruding, hard calyx teeth. Some temperate species of *Salvia* show this, and also tropical species of *Leonotis* and *Hyptis*. It is curious that such *Hyptis* spp. [*H. brevipes* and *H. rhomboides* (*capitata*)], have burrlike pseudoheads and that their nuts do not produce the mucilage of *H. suaveolens* (see p. 78), a species with flowers that are plainly axillar. The demarcation from rain-ballists (see p. 72) is to be determined after careful analysis of the following group, which possess queerly deformed, more specialized calyces. Some species of *Teucrium* and *Scutellaria*, as well as *Salvia glutinosa*, have a postflorally enlarged calyx with a springy pedicel and a kettle in which hairs keep the loose nutlets in position while at rest. In *Scutellaria altissima* the upper lip of the closed calyx has, according to Nordhagen, the tangent (the part receiving the shock) in its "scutellum". The whole upper lip is then thrown off the kettle along with the seeds (see Fig. 19).

Stopp (1958 a) found the same type of queerly dehiscing fruiting calyx in ballistic species of *Aeolanthus* (a Congolese Labiate).

Teasel (*Dipsacus*) is said to belong here for near dispersal, but it also spread through North America along waterways and the diaspores float. Nordhagen included some leguminous pods of Scandinavian *Oxytropis* species (*O. lapponica* and *O. deflexa*), where wind and raindrops are said not to be able to operate the ballistic mechanism (humidity disturbs springiness) and where reindeer can dislodge the firmly arrested seeds. Also to be included here are species of *Tiarella* (Saxifragaceae), *Vella* and *Carrichtera* (Cruciferae) with queer siliquae (see Fig. 20) in which the curious sterile beak has grown out as a tangent, transmitting the force to a critical spot. Thus an active explosion partakes in the ballism. Wild *Sinapis alba* shows this for the lower part of the pod. The upper seeds (much rarer) remain in the beak, which is loosened apart. They possibly germinate under different conditions. Other Cruciferae with spreading, but not explosive, pods use some disturbance from outside for initial, basal splitting of the valves.

#### 4. Creeping Diaspores

When dry and humid weather conditions alternate, the hygroscopic bristles of many diaspores can perform movements. Insofar as this leads to penetration into the soil, so well known for *Erodium* spp., the phenomenon belongs in the chapter on establishment (p. 116). In some species of *Trifolium* – as well as in many Dipsacaceae, Compositae and Gramineae – the bristles of the anemochorous calyxpappus or the awns produce (according to Ulbrich) by their movements some creeping of the whole (see Fig. 24). Their position would allow movement in only one direction. The comparable ones on pointed achenes of desert *Chardinia* and *Geigeria* in Compositae provide perhaps a parallel with drilling *Avena*, although the awned pappus scales are not hygroscopic and drilling has

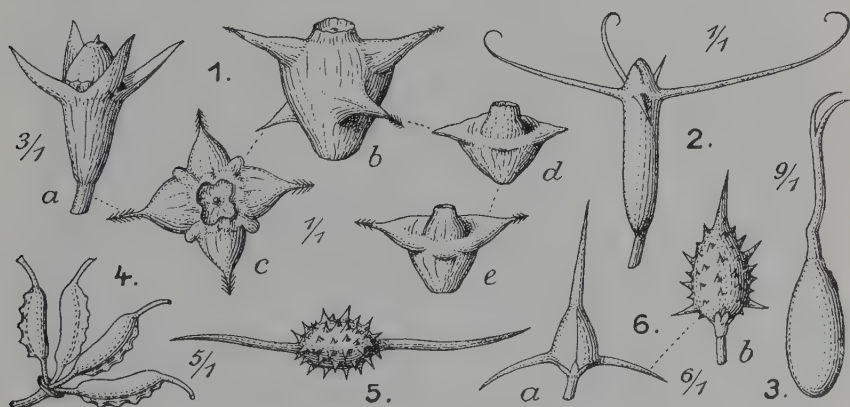


Fig. 21. Water burrs. 1 *Trapa natans* 2 *Trapella sinensis* 3 *Zostera marina* 4 *Zanichellia palustris* 5 *Blyxa echinosperma* 6a *Ceratophyllum demersum* 6b *C. submersum*. (Ulbrich, 1928). (Correction on *Zostera* in text)



Fig. 22. Coconut germinating on the shore of the new island Anak Krakatau among the drift, 10 years after origin of the island. Behind it *Spinifex squarrosus*. In the background young trees of *Casuarina*

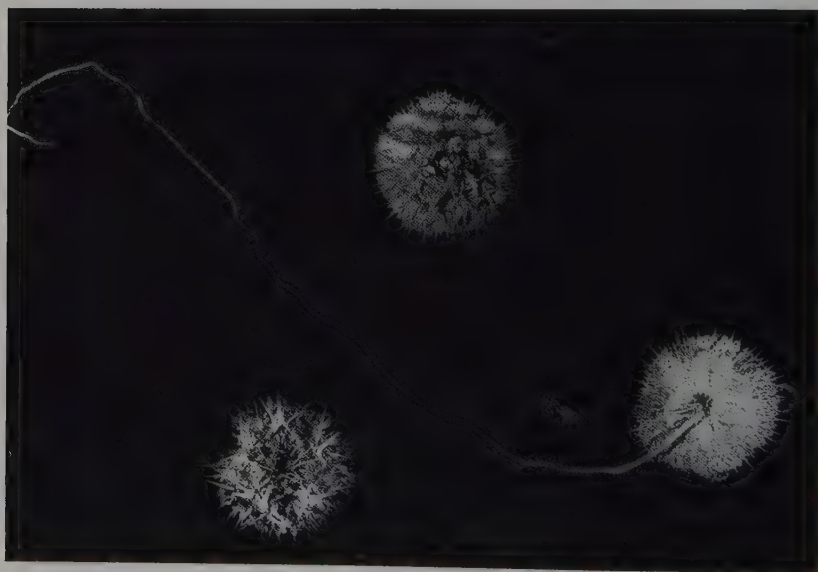


Fig. 23. *Neurada procumbens*. Woody, spiny hypanthia, one with lower, smooth surface up, showing taproot which has pierced opening. (Photo Natan)



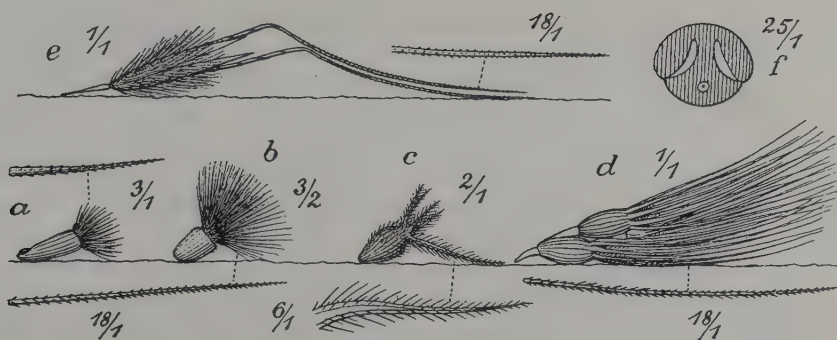


Fig. 24. "Creeping" diaspores, with the ends of the bristles magnified. Direction of movement to the left. **a** *Centaurea cyanus* **b** *Crupina vulgaris* **c** *Trifolium squarrosum* **d** *Aegilops ovata* **e** *Avena sterilis*. (After Ulbrich, 1928, corrected in the text)

not been observed here. A stiff small pappus may also bring the scar of the achene into the right position for uptake of water. The pappus of some *Centaurea* species is also too small for anemochory, but creeping is said to help in the seed dispersal in combination with ballistics and myrmecochory. I have not been able, however, to find any appreciable hygroscopic movements in *Trifolium lagopus* and *Tr. stellatum* or in material of *Aegilops ovata*, where only one subspecies may be a borer (Zohary in Baker and Stebbins, 1965). Datta et al. (1970) have confirmed that its units are atelochorous. The creeping of the figured *Avena* diaspores on a table cloth after alternating moistening and drying (in *Corynephorus* even hopping) is a funny sight, but on uneven sandy soil drilling-in is the main result. *Aegilops* diaspores will prove (in the chapter on grasses) generally to be moved only passively by wind as "wedge fruits". Creeping of 37 cm a day on smooth soil has been observed in diaspores (with a hygroscopic awn) of *Arrhenaterum elatius*.

## M. Barochory, Dispersal by Weight Only

The term (from "baros" = heaviness) is not entirely satisfactory, implying not only that the diaspores have no other means of dispersal, but also that they can roll away by the impetus of their weight. The plants that authors commonly place in this group make a rather chaotic and incoherent list (*Rhizophora*, *Quercus*, *Juglans*). Müller-Schneider even includes some myrmecochores, in which the bending to the soil is just a presentation of the diaspores to ants. The dropping of heavy pods for ruminants is also just presentation, not barochory.

The class forms one type of Dansereau and Lems (1957), which includes those cases where means of transport are only seemingly absent, in reality being just invisible at first sight. *Cocos* is also included here.

If we maintain the class, *Aesculus hippocastanum* is a convincing instance (see p. 30) and also perhaps some large leguminous seeds, as long as we find no

properties indicating a specific agent. We may suspect that *Castanospermum australe*, with its chestnutlike seeds, is in this category: the diaspores seem barochorous until we discover that not the diaspore but the parent fruit is specialized – an efficient ballist. Its frequency on stream banks in North Australia is due to collateral floating power. Another possible case is that of the South American *Mora* (*Dimorphandra*), which exhibits one of the largest seeds in existence ( $12 \times 7$  cm). As it is flat, it does not roll, so has absolutely no dispersal: achory (see p. 92) has been assumed. Seeds can, however, float in the swampy habitat near estuaries. They do, after inundation, reach the sea, although no longer viable (cf. *Entada*). We shall study abandonment of dispersal in favour of letting local seedlings wait for an opportunity, in the section on the rain forest.

## N. Retrospective View

It is tempting to try a comparison of dispersal spectra in all families and to connect it with phylogeny. We placed several loose remarks in this direction: the predominance of biotic connections and the rarity of epizoochory and autochory in old groups etc. There are, however, complications in the situation, ecological consequences of familial habitats to be discussed first, autonomous morphological possibilities in floral structures to be considered, etc.

We shall, moreover, have to await a chapter on general evolution of fruits and an evaluation of a proposed region of origin of angiosperms in general; and then we have to limit our review to the most important and varied families.

## VI. Dispersal Strategy and the Biocoenosis

As is fitting in a textbook, we started with autecology, the study of the individual species in relation to certain environmental factors. We stressed clear-cut cases of relation with one specific factor, to allow an orderly review as well as the recognition of natural divisions. Although ecological principles were also presented, the pigeonholes were necessary for general orientation.

It is now time to recognize coherently that this was an oversimplification, that in nature the environment works as a whole, that vegetation and its animal inhabitants are ecosystems with internal coordination; also, that each process has a counterpart which acts as a regulating brake and that in nature synecology is at work, with multiple internal connections. It is now customary in population dynamics to distinguish between opportunistic spp. with r-selection for unpredictable, open habitats and those with K-selection for competition in stable habitats. This complicates any discussion on selective value of dispersal though we find stability in open deserts.

It also becomes more difficult to discuss dispersal as an isolated process. In all biology there exists the choice between few large, well-provided-for and numerous small, uncared-for progeny. Dispersal strategy means a compromise between conflicting demands, including energy expenditure. It is part of overall population ecology and population dynamics. The strategies differ in annuals and perennials, in regard to short and long generation time, in continents and islands, in open and closed vegetations (see Salisbury, 1942). Dioecy and self incompatibility promote adaptive plasticity but limit colonizing dispersal by pioneers. Size implies some compromise between dispersal-capacity and liability to predation, also between easy dispersal and size of seedlings, next to other factors of establishment to be discussed in Chapter VII.

### A. Atelechory

#### 1. General

This is the occasion to introduce a concept which has general importance, although it has usually been treated for one kind of vegetation only, the semidesert. In contrast to the usual dispersal, which tries to cover long distances and conquer new habitats, we now see (and will come to study) the avoidance of too much or any dispersal and the inhibitory mechanisms for obtaining this. Establishment may prevail over dispersal.

The category may be called "antitelechory", "atelechory" or "achory" (not or not-far wandering). The Israeli botanist Zohary (1962), a specialist on the subject, switched to the term "topochory". This means "wandering on the spot", which is a contradiction in terms, so that his word might better be replaced by "achory", no dispersal. If he means to stress the liberation of diaspores on the spot, the prefix "topo" should be used in the combination "toposporry". We were forced to recognize the necessity of some atelechorous mechanisms earlier, when we were discussing anchoring in deserts under trample burrs; also, when we were discussing hydrochory and the danger of dispersal by wind to unsuitable habitats in the case of orchids (p. 62). I pointed (1957 b) to the same danger for *Sonneratia*, brought as an immigrant by sea currents to Riu Kiu but possibly unable to reproduce there because of the lack of pollinating bats. Further synecological research might show more cases of harm by dispersal outside the natural community. The rain forest will also demonstrate this (see p. 103). Recently even an atelechorous *Asplenium* (indehiscent sporangia) was found, limited to a highly specialized, small habitat.

The more limited the suitable habitat, the greater the waste. *Epilobium* (*Chamaenerion*) *angustifolium* is limited in this way to newly opened-up spots in forests and residential areas. Thanks to the "waste" in anemochory it appears immediately, like a microbe on its substrate. When no climax forms can suppress it, this species persists by means of subterranean buds.

There exists, however, a different strategy, the limitation of dispersal to the already occupied, obviously suitable spot. This is defensive strategy, avoiding useless waste in the wide desert. It may also be expected in alpine regions with limited suitable habitats.

Though some of his assumptions had to be criticized (on p. 80), Stopp (1958 b) has made an important contribution on atelechory in South African deserts. Partial atelechory will be discussed in the section on hetero-diaspory (p. 98).

Zohary mentioned in his book *Plant Life of Palestine* (1962) ten types of atelechory: baryspermy (our barochory), carpospermy (monospermy without dispersal), synaptospermy, myxospermy, trypanocarpy (boring diaspores), hydrochasy, basicarpy, heterocarpy, ampicarpy, vivipary and geocarpy. We shall discuss some of these categories separately and add to his trypanocarpy and myxospermy the other anchoring devices.

## 2. Synaptospermy

Murbeck (1919/20) describes the keeping or even bringing together of many seeds until germination as synaptospermy, or a limitation of separation. He has found the phenomenon convergently in plants of arid North African regions in 140 cases (mostly annuals), in contrast to five in Scandinavia.

The simplest case is non-dehiscence of many-seeded fruits, but in others, such as species of *Beta*, *Spinacia* and *Forskahlea*, the spiny or woolly fruits of the entire inflorescence stick together.



In the Oriental desert composite *Rhanterium epapposum* the dropped fruiting heads are synaptospermous. Though somewhat less clearly epizoochorous, they form a parallel to *Neurada* (p.80), also in the position required for germination (Thalen, 1979).

Murbeck admits that it is generally disadvantageous for many seedlings to stay together but thinks that this is less important in open vegetation. He states as the main local functional significance, confirmed by actual observations, that extra-envelopment offers better protection in the long dry period; furthermore, the complex prevents too rapid drying out during the all-important germination period; and, last but not least, the tissues of the complex can, during germination, hold more absorbed rainwater than isolated seeds can. He admits that the matter has other, accessory aspects, viz., better anchoring of the whole in the sand as a brake (the diaspores are often spiny) and a special dispersibility by the spines, though synaptospermy as such is not considered as designed for dispersal.

When synaptospermy is accompanied by variation of germination requirements inside one unit (heteroblasty) the mentioned disadvantage is annihilated, as shown for *Aegilops ovata* by Datta et al. (1970) and for *Tribulus* by Monod (1974 b). The two caryopses from one unit of *Avena sterilis*, also differ in germination potential.

Having observed that in *Beta* and similar forms the complexes are tumblers which catch more wind than single diaspores, and being also aware of the fact that so many cases mentioned have trample-burrs and adhesive burrs, I think that Murbeck has neglected the dispersal effect somewhat. The detachment of the whole complex also belongs to the syndrome of these diaspores. This aspect may very well have another background. The cited cases of synaptospermy in indehiscent, many-seeded pods of *Prosopis* and *Zizyphus* just point to dispersal by ruminants (non-dehiscence) and have no relation with atelechory, so that the high percentage of synaptospermy loses in significance.

The germinating together may also have a relation with stimulative physiology and with the breeding system (with incompatibility) and with little mobility or paucity of pollinators. These aspects deserve investigation. In Baker and Stebbins (1965, p. 170) it was pointed out, for a form of *Raphanus sativus*, which became weedy in California, that synaptospermy compensates for the handicap of self-incompatibility for a weed. Astley and Ford (1981) confirmed this for wild *Spinacia* spp.

We know of no work on atelechory in other continents. Zohary (1937) investigated the phenomenon for Palestine. He found it in 243 species, spread over many families and then in special subgroups. Instances are desert grasses (some spp. of *Aegilops*, *Triticum*, *Pennisetum*), Leguminosae (pods of *Medicago*, *Astragalus*, pods and heads of *Trifolium*), Composite heads, indehiscent Cruciferae (especially Brassicaceae), fruit-calyces of some Labiatae. He admits that synaptospermy is not *in toto* simply atelechorous. In Compositae, it leads to the disappearance of the pappus and in many other cases to monospermy of the fruit proper, as in the burrs of the Crucifer *Clypeola*, the spikelets of *Aegilops* and the

legumes of *Trifolium*. In considerations on the origin of Compositae this aspect cannot be neglected.

### 3. Basicarpy

The formation of fruits immediately above ground level is seen in many plants from semideserts. The older authors called it "hypogeocarpy", but Murbeck (1919/20) introduced the newer term as part of the atelechorous syndrome, as its protective aspect.

Stopp (1958 b) called attention to basicarpy in the South African desert flora, describing grasses (species of *Enneapogon*, *Cleistogenes*, *Stipa*, etc.) with partly basicarpous spikelets, the latter bradysporous and heavily protected during the rainless period.

Basicarpy as a mere phenomenon occurs elsewhere and may have a function totally different from waiting in a protected position, as in deserts. It occurs in Zingiberaceae in rain forests and may there functionally belong to the field of pollination. We have already discussed basicaulicarp in the section on reptile dispersal in Chapter V.

### 4. Geocarpy

The burying near the mother plant of all diaspores (geocarpy) or of a number of them (amphicarpy) is a very effective method of ensuring atelechory. In the older literature, where only distant dispersal was considered important, geocarpy was thought to be functional only as a protective device, directed especially against grazing animals. However, it is immediately clear that it can keep desert plants (mostly annuals that have to grow from seed year after year) in the right spot in an inhospitable environment. A review of old and new data was given by Hylander (1946). His seven types illustrate their divergence in ecological significance.

For Palestine, a dry country, Zohary (1937) listed many species (mainly Leguminosae) with amphicarpy. In the whole world, about thirty species are known with this character, a phenomenon still in development, and furthered by diverse means, in various families. Amphicarpy is often subject to phenotypic variation. It has some connection with floral cleistogamy, a connection absent in full geocarpy. Ulbrich (1928) discusses many cases, mainly European species of *Viola*, *Vicia* and *Lathyrus* (in the latter two cases, species growing in arid regions), and for America *Ranunculus hilairea* (Andean dry regions) and *Cardamine chenopodiifolia* (Argentina and Brazil). I must remark that the North American plant *Amphicarpa bracteata* (the hog peanut) does not grow in an arid environment; the deviating, buried pods are transported and cached by squirrels. The vernacular name is due to the fact that hogs also dig them up. Included are some grasses, even perennials, and some species of *Commelina*, not always desert plants. Stopp (1958 b) studied the amphicarpy of some South African desert species or races, the geocarpous fruits, as always, having a reduced seed number.

In the Gramineae (p. 181) and also some Cyperaceae, it may concern aerial fruits besides basal ones that are different in form and protective envelopes. In *Schoenoplectis* spp. the basal flowers are chasmogamous with a very long, protruding style. The inundation alternates with desiccation in their habitat.

Full geocarpy is rarely found in fruits produced from flowers that were already underground. However, it does occur in this way in some Palestinian Araceae such as *Stylochiton* and *Biarum*. Lists of geocarps by older authors do not always differentiate between geocarpy, amphicarpy and basicarpy – and between the different ecological classes to which the respective cases belong, as illustrated below.

For Palestine, Zohary described five cases (there are sixteen in the world); his description includes their physiology. Involved are some Leguminosae, but also a *Callitriche* found in temporary pools. The number of seeds in the fruits or the number of flowers in the heads is reduced, and dehiscence fails. The bestknown cases are some Leguminosae such as *Arachis hypogaea* (wild in mountainous parts of Bolivia,) *Astragalus hypogaeus* (West Siberia), and some Cruciferae such as *Geococcus pusillus* from Australian deserts. Other groundnuts, such as *Voandzeia subterranea*, *Kerstingiella geocarpa*, have been found in the wild in dry savannas of North Cameroon.

To consider geocarpy only in relation to atelechory in deserts is again simplistic. The subterranean clover (*Trifolium subterraneum*) occurs also in France and Britain. It even has strong colonizing tendencies, as became evident in Australia (Morley and Katznelson in Baker and Stebbins, 1965). Some of the fruits are dispersed as burrs and rollers; also, as in other species of *Trifolium*, achenes are eaten and dispersed internally by grazing animals. That the species is relatively favoured in a community by grazing may even be due to the ancient aspect of protection of the buried part of the fruits. In the Orient, some related species with less well-developed geocarpy occur.

Though there is a marked preponderance in arid regions, the phenomenon of geocarpy (as demonstrated already for amphicarpy) occurs also in moist habitats, which points to a different function there. South African *Falkia repens* (Convolvulaceae) grows along water.

The phenomenon also occurs in rainy tropical regions e.g. in Indonesia in *Cyrtandra* spp. The African rain forest has a *Begonia hypogaea*, growing near creeks and producing berries. In geocarpous species of *Ficus*, the phenomenon has an entirely different background (see p.27). The case of *Cucumis humifructus* has, although the plant lives in deserts, a connection with dispersal by digging animals that live underground (see p.54). The many-seeded fruit cannot be atelechorous.

A curious case, resembling *Begonia hypogaea*, where the ripening berry is buried by the bending flowers, was reported to me by Dr. H. C. D. De Wit (Wageningen). *Cephaelis (Uragoga) densinerva* (Rubiaceae) is a tall shrub growing on the margin of forests in Cameroon. The stalk of the inflorescence, in its upper part, grows down to the ground as a rope up to 4 m length. It is there among the debris that the small flowers open and the berries develop later on. It

has yet to be determined what this signifies, either for the flowers or the fruits but a comparison with *Plocama* (p.26) comes to mind. In relatives (classed under *Geophila*, *Psychotria*, *Cephaelis*), especially in *Geophila macropoda*, such a peduncle arises at ground level from the main stem.

The simple inclusion, in lists of geocarpous plants, of myrmecochores with fruit stalks that bend down, or even considering such presentation to soil or ground animals as "pseudo-geocarpy" (Ulbrich for *Cyclamen*), increases confusion. In the amphicarpous species of *Viola* (*V. hirta*, *V. odorata*) the "geocarpy" is clearly a further extension of such presentation. The plants are myrmecochores from a moist habitat.

An entomologist considered geocarpy in Leguminosae as an escape from bruchid beetles and bugs. This factor is important for the survival of tropical leguminous seeds (Janzen, 1969 b), but one might argue that oviposition by beetles may occur before burying, as observed in *Trifolium subterraneum*.

## B. Polychory and Attendant Phenomena

### 1. General

In the foregoing sections we have met many cases where diaspores are dispersed by more than one agent. This is designated as diplochory or even polychory, in contrast to the normal case of haplochory. Sometimes the "legitimate" way, as indicated by the condition of relatives and by remnants of adaptive structures, seems superseded by utilization and new development of some other character, which may originally have been incidental.

In this section, we shall again see that often consideration under a single heading or caption is unrealistic. A special character, then, proves important not only because it is directed towards two agents but also because it is connected with something that lies outside the sphere of mere dispersal. It then possesses two aspects relevant to two different fields of life. One aspect may be connected with the phenomenon of establishment, occurring later. Here, our classification by agents seems simplistic and invites replacement by one according to the destination of the diaspore. This would fit the later habitat of the plant. In many desert plants, the hard burrs that are observed so frequently show the apparently contradictory aspects of being dispersed and being anchored. In some shore plants (*Cocos* c. s.), we find two aspects to be considered: dispersal and arrival on a dry shore. In the cases of *Spinifex* and *Agropyron*, described in this book, the diplochory is of vital importance. The combination again means a refinement, harmonious, integrated, directed dispersal, somewhat along the lines followed in pollination. For shore and desert plants we shall discuss this cooperation in regard to the habitat under the heading of establishment. We do this, in part, to justify our hold on this field.

Self-anchoring water burrs or seeds with flotation slime may stick to birds' feet. On the other hand, real burrs of *Xanthium* may actually be water-dispersed



to and anchored on river banks. In *Bidens* spp. Lhotska (1968) describes the polychory of some neophytes, viz. endozoochory, regular epizoochory and also rapid downstream hydrochory. In some regions the berries (more acid there and described on p.34) of *Hippophaë rhamnoides* are not eaten by birds, but shrivel and drift about over ground, snow and water, propelled by the wind (Müller, 1955). One may wonder what happens to the germination inhibitors present in the pulp.

On the other hand, the marsh plant *Calla palustris* is not only endozoochorous and epizoochorous (see p.78) but also hydrochorous by means of floating, finally liberated seeds. Berries in transition towards myrmecochory (*Trillium*) may profit from two agents with different, complementary functions, as is the case in many other myrmecochores. The anemochorous fruits of *Acer* have been found in caches of rodents, where they germinated. *Alnus* spp. and *Aster tripolium* are anemochorous as well as hydrochorous. In cases of diplochory, different ecotypes may express different preferences. Sometimes the combined structural possibilities, together with a broad vegetative tolerance, lead to two different possible habitats. *Ximenia americana* is sometimes found as a seashore plant (due to flotation of the kernel), sometimes as an inland plant (due to dispersal of the drupes by pigeons). *Mimosa asperata* is found in its native Amazonia and in Java on river shores as well as on dry fields along animal trails, due respectively to the floating and the adhesion of their spiny joints. Such cases demonstrate the influence of dispersal on distribution and speciation.

In 1957b I described quite a number of plant species that entertain connections with both bats and the sea; *Cycas rumphii*, *Calophyllum inophyllum*, *Hernandia peltata*, *Terminalia catappa*, *Inocarpus edulis* and species of *Pandanus*. The bond with the sea is the secondary one, although it is important for distant dispersal and colonization; the one with bats takes care of inland settlement. *Morinda citrifolia*, *Hippomane mancinella* and *Phoenix palustris*, as well as others, might be added. In these plants the twofold dispersal has a curious synecological aspect. Sea currents bring them to the shores of islands, but bats and birds that can live on the fruits transport them inland. This provides an answer to the sophistic question: which came first, fruit-bats without fruits or bat-fruits without bats?

*Sonneratia* has a berry, eaten for example, by bats. It is bouyant (eaten by fish) and exposes its heavier seeds after decaying when stranded.

*Cassytha filiformis* (Lauraceae) is pantropical on beaches, due to its floating seeds, but may occur inland due to ornithochorous fruits. Island biogeographers had to reckon with harmony between immigration of fruit-plants and fruit-birds, also of host-plants for insects and insect-eaters. Frugivores may be relatively rare here in comparison with (more generalized) seed-eaters.

The synergy between the anemochory and synzoochory of *Pinus* and the dispersal of *Quercus* was discussed on p.31.

Some authors speak of collateral zoochory or anemochory. A wealth of terms may be coined in this field by lovers of term-manufacture.

## 2. Heterodiaspory

Polychory does not necessarily mean that every diaspore may avail itself of several different methods of dispersal. The plant may avoid putting all its eggs in one basket in other ways. Its seeds may show convergence with spores (micro vs. macro) and gametes (anisogamy) in reaching differentiation in cost, size, risk, precision, mobility and germinability. One method consists in differentiation in structure of its diaspores, another in differentiation as to time of presentation and/or germination. The first method may lead to amphicarp, a situation where both aerial and subterranean fruits are produced. This differentiation leads to the development of one kind of diaspore for dispersal and another for defensive nondispersal, as mentioned under atelochory.

Another differentiation produces ordinary heterodiaspory (heterocarp and heterospermy) with both kinds of diaspores functioning in dispersal, albeit dispersal by different methods; one of these serves mostly for limited, synaptospermous dispersal. This is the most frequent method in plants from arid zones, where a reserve is kept to bridge an unfavourable period. The phenomenon is found in the "weedy" families, viz. *Chenopodiaceae*, *Gramineae*, *Leguminosae*, *Cruciferae* (Voytenko, 1968) and *Compositae*, the specialists in dispersal refinement. In some cases the differentiation is under the control of environmental cues. For phylogenetical considerations see Zohary (1937). Grasses are discussed on p. 95 and p. 181.

Heterodiaspory is more or less limited to annual, weedy plants from open, arid vegetation.

In the *Compositae*, heterocarp has been investigated by Becker (1913). There is an apparent basis for its development in the difference between outer and inner flowers in the capitulum, but Zohary (1950) has shown that the differentiation in fruits is often of independent origin, especially arising in *Liguliflorae*, etc., without differentiation in flowers (cf. Burt, 1961, cited on p. 18). The general impression is that the outer fruits in those cases tend to be without speedy dispersal structures and stay in the involucre the longest and are sometimes spread late within the dropping head, thus are synaptospermous, according to Zohary (1937), while the inner ones are built for earlier, faster and farther dispersal, being provided with pappus, wings and hooks. So it is in the American genera *Ximenesia*, *Gutierrezia* and *Synedrella*, and in the Mediterranean form *Rhagadiolus (Hedynois) creticus* (see p. 79). *Calendula* there produces three kinds of diaspores, all from the spirals of ray florets. The inner achenes and the winged (anemochorous) median ones drop easily from the fruiting heads that curl outwards. The outer, spiked fruits remain attached and form (separately or in combination) a kind of burr. The three fruits have, according to Becker, different germination requirements, but in my room they germinated equally in the following year. The small inner fruits turn dark between the still yellowish outer ones. Being pupa-like (larva fruits) they suggest insect mimicry towards birds (not ants).

Burt (1978) analysed composite heterodiaspory further, relating it to processes in population dynamics and adding cases where complete capitula are heterosporous. Evenari (1963) described a *Gymnarrhena* with the special, basal heads subterraneous.

*Xanthium* and other genera show, in addition to a slight morphological difference of no direct chorological consequence, a difference in the time of germination between the only two fruits contained in the detached capitulum. This leads to a differentiation that will be discussed later. Becker (1913) has shown that in this and other cases the difference in germination is due to the difference in pericarps, so that the plants have no heterospermy proper.

When the pericarp or accessory parts contribute substantially, the distinction between seeds and fruits is not merely academic, as is shown also by the variability in size of such "seeds".

Physiologists have emphasized here a causal explanation, stressing the different origins in time (day length) and place (see Goebel, 1913, p. 431). The question remains why this influence reigns only in these special species and regions. In the *Aethionema* described on p. 72 the deviating upper fruits arise independently of seasons and are not only unwinged and indehiscent, but also lack myxospermy. They point to an ecology without water as an agent, in contrast to the winged siliculae. Zohary (1949) already described this for *Alyssum* spp.

For Palestine, Zohary (1937) has given a list of 100 cases (all annuals but including families other than the Compositae) where the retarded diaspores provide atelochory. Cruciferae (*Heterocarpus*) and Leguminosae (*Desmodium heterocarpum*) join in. In some *Rumex* species basal and higher-placed fruits differ in form. Here, germination in the two types is about the same, but the seedlings differ in size (Harper in Baker and Stebbins, 1965). Strong heterocarp exists in the Mediterranean species *Fedia cornucopiae* (Valerianaceae) which has three astonishingly different kinds of fruits on the same plant, others on related species (better indicated as fruit polymorphism) leading to strong polychory by their anemochorous (p. 69) epizoochorous, hydrochorous and myrmecochorous properties (Sernander, 1906, 1927). Levina (1967) has published (in Russian) a review of many papers on the subject, that have been published in Russia.

Zohary (1937) lists cases in Palestine of a different phenomenon, heteromerism, where the two parts of one fruit are different in form and function, one part being atelochorous in most cases; cruciferous species of *Cakile*, *Rapistrum* and *Sinapis* (see p. 87) are well known in this regard. Voytenko (1968) has analyzed these cases.

A third term, heterospermy, is applied to differentiate among the seeds themselves, a phenomenon known of old in *Spergularia marginata* and Chenopodiaceae. Zohary has investigated this for Leguminosae with seeds diverging in time and power of swelling, over a spread of some years. Harper (in Barker and Stebbins, 1965) reported on heterospermy in weeds with (I fear) an agriculturist's disregard for the differences between seeds and fruits. In *Chenopodium album*, four types are borne on one plant, their difference in

germination assisting the species in aggressivity. Purely physiological heterodiaspory (the heteroblasty of Evenari, 1949), often connected with differences in situation on the plant, may be frequent.

Datta et al. (1970) analyzed the germination of the diverse grains (also differing in size) in one compound diaspore of *Aegilops ovata*. One germinated after rain and one after prolonged wetting, while others had to wait for disintegration. Zohary (1937) and Monod (1947b) reported the same for the (apparently equal) seeds in few-seeded trample-burrs (including those of *Tribulus terrestris*). In some of the Composites mentioned above, the disk achenes may germinate immediately under different conditions, whereas ray achenes may require afterripening and also specific cues from certain conditions. Relict seeds may also better survive predation.

Opinions differ on the question as to whether such differences in germination have led to morphological heterodiaspory – or if the sequence has been the reverse.

The term “seed polymorphism” has been used here indiscriminately. In my opinion it should be reserved for within-species strains with genetic differences in seeds. *Aegilops speltoides* has two kinds of diaspores borne on genetically different individuals. Sterk and Dijkhuizen (1972) found that winged and unwinged seeds in *Spergularia* spp. were genetically determined. In different habitats selection promotes different seed types. The habitats are not xeric. Here the polymorphism does not result so much in different dispersal, but more in different seedlings.

The germination of apparently uniform seeds in flushes and under different conditions has also been called polyphenism. Such heterogeneity may (outside mere deserts) be of importance to studies in population genetics, as it allows variability according to habitats.

For old, enumerative descriptions of heterodiaspory I refer to Delpino (1894) and Huth (1895).

### 3. Tachyspory

The foregoing cases lead up to the mentioned differentiation with time among diaspores; differences become manifest in time of presentation, dispersal and also germination, a field at first sight not within the area of dispersal proper but not separable from it in practice, in the ecosystem. We saw the importance of rhythms.

For our purposes, it is necessary to refer to some classical terms. Sernander distinguished tachysporous plants (“tachy”=fast), where the diaspores are set free immediately after maturation, and bradysporous plants (“brady”=slow) where liberation comes only after a long delay. The delay can be one winter (“Wintersteher”) or one summer, or some indefinite period (macrobiocarpy) as in spp. of *Pinus*, *Callistemon* and many Proteaceae (see p. 123). The most extreme cases of macrobiocarpy are found in a ragweed (*Ambrosia bryantii*) where the thorny involucre remains imbedded in the plant for some seasons, and in *Pinus*



*attenuata*, where the cones stay on the plants and are overgrown by the bark, so that their seeds come free only at the death of the tree.

The fruiting heads of *Gymnarrhena micranthia* (p. 99) remain buried in dead remnants of the mother plant for years.

In periodically dry regions the timing is often provided by xerochastic opening of the containers (in anemochores and ballists) or by hygrochastic opening when humidity is the necessary signal. The fruiting calyces of Labiatae, the study of which by Stopp (1952) should be followed up, vary strongly in this respect; they are important organs in dispersal. Many desert plants with heteromerocarpy have, in one and the same fruit, bradysporous and tachysporous parts. Zohary (1937) analyzed this for Palestine, Stopp (1962) for some Pedaliaceae in Angola. Many desert Mesembryanthemaceae strew seeds only when rain comes (hygrochasy), with ensuing weak ombrohydrochory. They retain part of the seeds in special pockets, curiously convergent in the diverse genera, to serve in later, distant dispersal (Ihlenfeldt, 1959) or as a reserve when a first, incidental rain had no follow-up.

Silicles of *Anastatica* throw off their valves after rain, liberating the myxosporous seeds.

## C. Concluding Remarks on Synecology

### 1. Deserts

We have seen on several occasions that the influence of dispersal reaches farther than the individual plant species and can characterize communities. In many treatises on deserts pollination, dispersal and germination are strongly underrepresented when compared to vegetative physiology. More ecological minds have presented us with details concerning the reproductive processes in addition to vegetative details such as geophyty, prostrate growth-form, etc.

To recapitulate some data from the foregoing parts: Murbeck (1919/20) found synaptospermy in 140 species of the arid North African flora, with 100 reaching into the Sahara. Zohary (1937) found the flora in Palestine to be 11% synaptospermous; this against the 2½% in southern France reported by Müller-Schneider and almost 0% in Fenno-Scandia. Murbeck found myxospermy in North Africa in 11% of the species, in true desert regions even in 20%, but in Scandinavia only in 3%. In considering such regions with their atelochory, one gets an impression of dispersal totally different from the one conveyed by textbooks that are based on the model of Western Europe. Our current views on cruciferous and leguminous fruits should also be radically revised for these regions, even to the extent of shedding new light on possible evolutionary processes in ovaries and fruits in general (see p. 145).

The main stability in this vegetation is not constancy but more resilience, due to elastic devices for survival under stress, with varied dispersal and triggered germination, variable in time and a reservoir in the soil.

A review of percentage importance of dispersal agents would be equally interesting, considering the many tumble-weeds, trample-burrs, heterodiaspory, etc. In a preliminary paper Monod (1974a) presented a kind of spectrum with an ad hoc classification that included presentation and fixation. Real endozoochory by fruit birds is here very rare.

Anchoring is achieved not only by the devices described for desert diaspores but also by depressions in the soil that are, moreover, slightly damper. Footprints of camels often show massing of seedlings. Monod found many diaspores, including grass spikelets, in the debris of eolic drift arrested in depressions. In the first instalment (1974b) of his more elaborate study he considered many species individually. Anemochory is, of course, prevalent.

Though the foregoing concerns mostly annuals needing reseeding, whereas American writers pay more attention to shrubs and trees, it remains remarkable that, in a special paper on the subject (Spalding, 1909) and in later monographs on North American deserts, we find no mention of the above-described characteristics except for the frequency of burrs. These desertlike regions also deviate from African counterparts in the matter of pollination (little myophily). Some anchoring in depressions and by shrubs is described, not achieved by special devices on diaspores. Contrary to atelochory, obligatory distantiation of new plants is described for some species of *Cotinus*, *Cercidium* and *Olneya*. This is achieved by germination of the seed only after it has undergone abrasion by drifting over the surface for some distance. Some timing of presentation by means of hygrochasy has been described, e.g. for the pods of *Acacia constricta*. This stands in contrast to the long list in Zohary (1937) for Palestine. For characteristics of phenology, dormancy, fixation, germination and seedling survival I refer to later chapters.

## 2. The Rain Forest

Our views on fruits and their evolution have also been changed greatly by considering tropical conditions, even though in recent years the impression has been created that dispersal and its organs are of no importance there, at least in the rain forest. (For the tropical seashore vegetation the great influence of dispersal is readily recognized.) Therefore we shall now turn our attention to reproduction in the rain forest. As a community, the rain forest is at the same time archaic and complex, stable and polymorphic, although its present distribution has not necessarily been permanent. It is a strongly homeostatic unity, full of feedback, and thus with a stable inner life governed by many influences. Its floristic complexity means there is a certain distance between conspecific trees, producing an independence from "pest-pressure", as already indicated by Ridley (p. 107), elaborated by Gillet (1962), Grant (1963, p. 421) and later on by Janzen (including 1970) with intensive study of the influence of predators on seeds. The study of seedling mortality also deserves further investigation. The rain-forest thus does not show exclusion of vicarious species,

though this circumstance does not justify the opinion that the struggle for life and interspecific natural selection is absent.

The review by Gray (1972) considering outbreaks of insects in tropical forests refers amongst others to papers by Atkison and Kalshoven. These, however, consider only deviating edaphic and climatic variants (mostly in Javanese monsoon forests and artificial plantations) of interest to agricultural entomologists. The insect-outbreaks observed by Gray concerned impoverished forests with dominant gregarious trees, also peat swamps. Mangrove stands can be decimated.

The complexity also provides flowers and fruits all the year round, with related species separated in time (Snow, 1966). McClure (1966) has found a differential selectivity in dispersal by birds and mammals, of which the squirrels *Ratufa* proved important fruit-eaters. The fruiting was proved to be often irregularly spread over years. This is quite a different situation from the condition in temperate forests, where fruit-eaters cannot always find food and where the herbaceous undergrowth has to offer some relief early in the season. We saw that even in vegetation composed of shrubs and herbs there, the continuity of food is not guaranteed, and that fruit-eaters can only temporarily subsist on their usual diet, switching (when necessary) to animal food or to dry fruits, the latter also fit for storage during the unfavourable period. Vertebrates subsisting on flowers are excluded unless they can migrate to the subtropics, which in Europe is difficult.

We have to leave aside the herbaceous undergrowth, often microspermous, rarely with burrs (see p.82).

Many of the points raised in this chapter had already been discussed by van Steenis (1958).

As said before, the fruit-eating birds and mammals of the rain-forest are not all arboreal. For tropical America we have data on the fruits and seeds dropped and (partly) consumed on the ground. In his "fruit traps" Smythe (1970) found a monthly average for Panama (g per m<sup>2</sup>) of 0.061 (December) varying to 1.93 (June). The large not-dropped arboreal consumption should be added to obtain an idea of such productivity. In Asia the latter consumption seems relatively larger.

In the rain forest, each plant species makes reproduction by means of resident animals possible for another species that flowers and fruits later on; this is true even if the later one is a congeneric species with competitive vegetative requirements. A similar situation exists with regard to pollinators. In this field, it is not only the highly developed specialists that should be considered as permanently present and bound to the forests as a whole. Archaic pollinators, such as beetles and flies, also show this bond, and even obviously, since they and their larvae (not being specialized for flowers) have to subsist on the living or decaying material of plants and animals in the whole community.

For dropped trample-burrs and the rare burrs in the undergrowth see p.82 and the chapter on grasses. Acorns and chestnuts originated here in South Asia at higher elevations.

The poorly developed dispersal potential of trees makes for a sufficiently uniform distribution within the rain forest and also for recolonization of adjacent "wound areas" (secondary vegetations in large gaps). After climatic fluctuations this had to occur on a grand scale. The large size of, and lack of dormancy in, seeds is connected not only with the special dispersers, but also with a special way of rejuvenation, viz. by the omnipresence of waiting seedlings, getting a chance in the small gaps mentioned (so-called advance growth). A few grow slowly and continuously. The long-term conservation of climax diaspores in the soil is much weaker than in secondary forests and temperate forests. The appearance of pioneers in large openings is thus not wholly due to dispersal. Their dormant seeds remain in the soil, as was also demonstrated for Mexico by Guevara and Gomez-Pompa (1972), including *Cecropia* and *Swartzia* spp. For Surinam this was elaborated by Ketelaars and Budelman (1976), who also studied dispersal, germination and succession in clearings.

We may justifiably be curious about the fate of reforestation experiments that start with the adult organization of climax trees and with pure stands. There exist local variations in composition due to edaphic influences (though this is not a dominating factor). Under marginal edaphic conditions (as in the mangrove) a special selection of climax forms or pioneers may be evident, resembling temperate "associations". Here one factor dominates.

I could illustrate the principle of "ecological parasitism" on the complex with the example of orchids utilizing pre-existent ecological niches, food, substrate and pollinators, but this is not the occasion (see under van der Pijl and Dodson, 1967).

Richards (1952) could originally maintain the concept of uniformity in the optimal rain forest because he neglected the biotic element and reproduction. Temperate sociologists were glad to find, beside the mentioned marginal "associations" in very poor conditions, some connections with their familiar concepts when they discovered "aggregates" of one dominant in some rain forests. These may, however, often be due to the fact that just one species was in fruit near an incidental gap, or had seedlings ready in it. According to Jones (1955) the aggregates contain young trees and are less obvious in regard to emergents.

In the following Table 2, I compare the climax forest with its predecessor, the secondary forest, which it succeeded after large-scale catastrophes. For a characterization of the latter see Richards (1952, p. 377–386). It shows some characteristics of the temperate forests, which are still more impoverished in species and especially in pollinators and dispersers. I must leave the zoological side to other ecologists. The table, neglecting gradations for the sake of simplicity, may seem somewhat superfluous here, but it can serve other purposes. The points pertaining to size, germination and rejuvenation, already touched on foregoing pages will be discussed in a subsequent chapter. In this regard we shall also find differences between the rain forest and the nomadic pioneer vegetation of the secondary forest. The parallel with K- and r-selection of zoological population theory is clear. They concern a saturated and a rarefied



environment respectively. Curiously, the only treelike Composite in South Asian rain forests, *Vernonia arborea*, does not belong to the true pioneers, though it still has rather small, pappose fruits. It settled late on Krakatau in existing woodland: in light rain forest it rejuvenates itself. Therefore it seems a successful intruder, not a form regularly killed by climax forms. In more respects the limits between nomadic pioneers and climax forms are not absolute. *Schima noronhae* in Java (with winged small, liberated seeds), *Ceiba* and *Ochroma* in tropical America, are transition forms. Some tall Leguminosae from the upper stratum of the climax forest, though not drought-resistant, can delay germination, e.g. the giant *Koompassia* spp. from Sumatra. They have soft seeds but thrive already in open, very young secondary vegetation, brought there via anemochorous pods from seed trees. A fire-resistant pioneer can outgrow young primary successors when fires destroy the latter. An instance is *Pinus Merkusii* (see p. 121).

A comparison between the rain-forest and the monsoon-forest yields comparable results (Baker in Meggers et al., 1973).

After this digression on inner coherence, we go back to simple characterization of the community from the viewpoint of dispersal. Perhaps the first published estimate in the direction of a dispersal spectrum was the one made by Stapf in 1894 on the forest of Mt. Kinabalu (Borneo): 35%–40% fleshy fruits, 25%–28% wind-dispersed, the rest unspecialized. The spectrum can, however, as Stapf showed, vary at different altitudes due to the influence of wind, which increases with altitude. In the different layers of vegetation it can also vary, but a

**Table 2.** Comparison between rain-forest and secondary forest

Secondary Forest	Climax Rain Forest
Total, new colonization from reservist seeds (nomads) after destruction	Permanent growth, local rejuvenation in gaps
Germination in light	Germination in shadow
Strong dormancy remaining viable in the soil	Weak dormancy
Seeds small	Seeds often large
Immediate outgrowth of seedlings	Seedlings waiting for a chance
Rapid and distant dispersal, much anemochory, many dry fruits	Limited dispersal, much zoochory, many large, fleshy fruits
No internal rejuvenation, life span limited by overgrowing or speedy reproductive phase	Constant rejuvenation, life span unlimited, layers and shade tolerance change
Very open to outside influences, more mixed and migrant visitors	Closed-off inner reproductive system, constant food production for pollinators and dispersers
Pollinators less dependent on living whole, specialized	Many archaic flowers for beetles and flies bound to whole for life cycle
Unstable, more open to pests	Homeostatic, more immune to pests

large percentage has no special means of dispersal. Richards (1952) pointed to the wind dispersal of some top-story trees.

It is, however, remarkable that in the highest mountain zones (at least in Java) the low forest is dominated by endozoochory in birds. In their open regions anemochorous herbs (grasses and orchids) prevail.

The rain forest of South Nigeria has, according to Jones (1956), in the emergents 46% of the species wind-dispersed and 46% animal-dispersed, but in the lower stories the proportions are 7% and 71% respectively. Keay (1957) found there in an old secondary forest the following percentages of wind-dispersed species: in emergent trees 56%, upper-stratum lianas 48%, upper-stratum trees 25%, lower-stratum trees 2%, shrubs, treelets and lower lianas nil. Herbs and epiphytes were not considered. All the cauliflorous plants produce fleshy fruits.

Later on, finer differentiations will become necessary, such as that between small- and large-seeded fleshy fruits, the first being more typical for bird-dispersed pioneers, the latter also for mammal dispersal.

Our observations on initial and mature stages agree with the general theoretical considerations in the final chapter of Margalef's book (1968), which are more zoologically oriented. As we shall see next, however, the use of mathematical models on equilibria seems too deterministic for communities that are in principle open.

This is not the place to go into deviating opinions on the relationship between diversity and stability, nor into those on different kinds of stability (see p. 101). Other factors are also decisive. The aggravating factor of poor fertility (cited as fatal for Amazonia) could, there, only delay new extensions of the rain-forest areas after climatic contractions and before the influence of man. Such shifts may have brought together many species of one genus arisen allopatrically, including pioneers that had occasion to adapt to shadow.

### 3. Epiphytes

In this component of the rain forest and other communities the transport factor plays a more dominant role, since the substrate requires special devices for arrival and settlement of diaspores.

In many instances (in open forests) we find simple anemochory with dustlike diaspores and plumes, often a transition from anemochory with some modification for attachment to the bark of trees. Many epiphytes, such as those in the large genus *Ficus*, have small bird- or bat-dispersed seeds sticking on the sub-stratum with the excreta; rarely (*Peperomia*) viscid, epizoochorous diaspores.

Even some epiphytic orchids (*Aerides*, *Ionopsis*) possess hooks on the seeds.

The group of ant-epiphytes was discussed on p. 59.

The absence of epiphytes among Leguminosae (in contrast to its many climbers) may be based partly on the seed-character of the family and partly on its lack of perennating vegetative organs, another point of importance for life as an epiphyte.

Heintze (1932/35) filled the two instalments of his book with data on European occasional epiphytes (tycho-epiphytes) and how they arrived in the crown of pollard-willows, etc.

#### 4. The Arctic

Savile (1972) discussed the unadaptiveness of conventional dispersal systems here for long-distance dispersal. Epizoochory and endozoochory suffer from the low animal density, although incidentally, the brant goose (*Branta*) complies. Plumed diaspores occur, but wings are scarce. Chamae-anemochory without obvious modifications is important over frozen water and snow in the winter. *Saxifraga* fruits are analysed in this respect. Some species are not relicts but seem to have been dispersed since the end of the Pleistocene.

#### 5. Island Floras

Although the analysis of further regional floras lies outside the scope of our book, we may make an exception for small, strongly isolated regions. There, one can study the transport factor intensively, and also the influence of long isolation of a new community on speciation; and, finally, the fitting together of immigrants in a new synecological whole. Some remarks on plant-animal harmony were already made on p. 97.

For a general (often mathematical) analysis see MacArthur and Wilson (1967). The actual dispersal, the factor of synecological coherence and botany as the basis of heterotrophic zoology remain somewhat in the background. Zoologists use in such mathematical treatments the balance immigration-extinction, but botanists have to reckon more with, on the one hand non-establishment, on the other hand less rapid extinction of whole populations – and with synergy. The book by Carlquist (1965) is of a much more popular nature.

The first instance of such an “insular” community (habitat island) is the one of isolated mountain tops. For such tropical South American “paramos” Simpson (1974) demonstrated further extension with better contiguity during glacial times. The tree line was depressed for 1500 m. These findings annihilate the here formerly assumed incongruity of area with species diversity and the too low vagility of plants for immigration. Loss of dispersability can be secondary, brought about by later isolation, just as in islands. Later publications demonstrated the same for the Indo-Australian regions where glacial periods in larger continental areas may have caused other currents and climates in tropical zones with more aridity and more open vegetation.

Stapf (1894) has pointed to the apparent lack of specialized dispersal mechanisms in the alpine region of Mt. Kinabalu (Borneo). For the Malaysian mountain flora as a whole, van Steenis (1933/36) has analyzed all factors that might possibly be responsible for the distribution of the orophytes (the non-tropical species). From the geological and historical factors that had to be

considered, he rules out any very profound influence of the Ice Age. He also excludes the factor of dispersal, on the basis of present-day data on dispersal. The isolated habitats of *Primula prolifera* (without apparent means of distant dispersal) are presented as illustrative, as is the occurrence of some summit plants with berries on a few mountain tops only (obviously denying local effects on ecesis). He doubts any effect of occasional events, such as cyclones. As we saw before, the riddle of the distribution thus remains unsolved in a causal sense.

Hedberg (1969) believes that cyclones have an effect on the formation of isolated mountain floras, which thus often become incidentally different in composition, though situated in the same region. One diaspore settled in fifty years is reckoned sufficient to explain this state of affairs. Wickens (1976) is, however, discontent with non-repeatable, low-probability processes, quoting much literature.

I note that zoologists have found in isolated islands or on mountain tops that the impoverished habitats may inhibit coexistence of species living together elsewhere. Incidental first arrivals or last remainers may exclude competing species of birds by lack of niche diversity. This circumstance may also influence plant distribution on mountain tops.

In a symposium (Constance, 1963) on long-distance dispersal of the many Western American disjuncts between North and South America, attention was paid to migrating birds as vectors. Proof remained vague. For a subsequent analysis see Cruden (1966). Stepwise dispersal ("mountain-hopping") was proposed. Such theories do not, in my opinion, take into account the necessity of intermediary local establishment and of local pollinators and dispersers. The same is true for "island-hopping" in the following part – on real islands.

Alas, far-migrating birds are rarely frugivores. Ducks do better. South-North American continental drift cannot be held responsible for the disjunctions. Simpson (1974) demonstrated that in general distant colonization took place principally during glacial periods.

Moore et al. (1972) studied some of the 30, far distant, practically identical bipolar species, (including those of *Carex* and *Plantago*). They must rather recently have crossed the tropics by long-distance dispersal.

Thorne (in Meggers et al. 1973) used harsh words against antagonists of this idea of dispersal in his discussion of distributional links between America and Africa.

The famous instance of the continental island of Krakatau and its new vegetation, though remaining of considerable interest, is of limited importance in the consideration of transoceanic transport. Its recolonization was, moreover, largely a matter of the increasing possibility of establishment on the substrate. In the beginning many more plants were transported over the short distance than became established. Even diaspores of inland plants were transported to the new beach and lived there for a time.

The old story of recapitulation of evolution in the changing vegetation there cannot be maintained as generally valid. For details of the succession and the transport see Ernst (1934) and Docters van Leeuwen (1936). Sea transport was



quickly saturated, soon leading to normal shore composition. Overseas transport by wind and birds followed, in that order. The diplochory of the plants mentioned on p. 97 (with dispersal by bats and sea currents) was helpful in establishing a community.

The more general synergy in the rain forest is clear from the continuing enrichment in species on Krakatau. This deviates from purely mathematical models, which reckon mainly with immigration and antagonistic forces.

As already indicated above, the (mostly zoological) rules of MacArthur and Wilson (1967) on saturation of a population should not be applied to plant communities. This is demonstrated by Whittaker (in Woodwell and Smith, 1969) for the vegetative sphere. Considerations on reproductive webs fortify this (van der Pijl, 1969) stressing not only, as usual, the flow of energy, but also the flow of biological forces and signals.

With regard to truly oceanic islands, opinions differ strongly on the possibility of long-distance dispersal: the discussion has become muddled by the introduction of (at the time) moot points concerning ancient land bridges, ancient continental boundaries, continental drift, etc. I pass over violent old disputes on this question. Ridley (pp. 674–690) tends to accept long-distance dispersal by birds and drifting logs, giving many cited cases as proof (pp. 28, 33). To mention some new instances: Taylor (1954) has found on Macquarie Island, 950 km southwest of New Zealand, 35 species of vascular plants. The island was once completely covered by ice and was never connected with larger land masses by bridges. The plants may all have arrived fairly recently with the aid of birds, by means of hooks and viscid berries. He reports such diaspores as actually being found on albatrosses. Endemism is practically absent.

The disjunct distribution of some species of *Uncinia* (Cyperaceae) on mountains in some Pacific islands, outside their centre in New Zealand, has been explained by Hamlin (1959). As the hooked utricles were found on migrating birds he accepts long-distance dispersal by them.

On the new island of Surtsey (Iceland) the first higher plant came by sea (*Cakile maritima*), but immigrant birds may soon have contributed, as shown on p. 33. The well-known cases of single ornithochorous species from American families (spp. of *Pitcairnea* and *Rhipsalis*), found in Africa, point in this direction. This distribution of modern, specialized plants stands outside the matter of continental drift, though at the time of the assumed bird dispersal the distance between the continents must have been shorter, especially in the North.

Fosberg (1948, 1951) has always been a protagonist of dispersal to oceanic Pacific islands by means of sea currents, jet streams and sea birds. He has attempted to determine the number of successful colonizations needed to account for their present flora. Of 1729 species of seed plants on certain islands, only 272 represent more or less the original immigrants. For their establishment, only one successful colonization every 25,000 years was necessary. Such rareness means also rareness of re-introduction, which circumstance allows independent evolution into a new species. Moreover, the disharmonic floral composition of the Hawaiian Islands (curiously without the primitive relics of old Pacific islands)

and which differs from island to island, is considered to be proof in itself. For Hawaii he postulates 69 species as a basis of development; of these, 21 remained in the original state, the other 48 giving rise to the remainder of the flora through later evolution. This now deviating component may even be partly derived from drift plants which originally possessed large floating seeds. The richness in easily dispersed ferns is typical. The absence of bats and large herbivores is reflected in the spectra of pollination and dispersal. The isolated Archipelago is estimated, in its different parts, as being between 700,000 and 2 million years old. Distant dispersal without land bridges and stepping stones must be accepted. Continental drift seems irrelevant here.

Carlquist (1967) has studied not the geographical sources but the possible means of arrival. He points to dehiscent berries of lobelioids (*Clermontia*), in which the pulp around the small seeds can provide additional epizoochory. He gives many other data on bird dispersal to oceanic islands.

Guppy (1906) has pointed to the increase in seed size after immigration on islands, and Carlquist (1966 a, b) has further developed this topic. After studying the means of transport, he defends long-distance dispersal as basic for Hawaii, as well as the evolutionary developments following immigration. The latter resulted in a low dispersal rate in a new stable vegetation. This represents not just the adjustment to "wind pressure", presumed for flightless island insects. The process of "precinctiveness", not ascribed to lack of furry dispersers but more in line with atelechory, was made evident for some Compositae in Pacific islands of overwhelmingly American affinity. Seed size increased, sometimes resulting in gigantism elsewhere (*Stenogyne*, *Tetraplasandra*); the hooks of *Bidens* decreased in size or disappeared.

Carlquist quoted its relative, the genus *Fitchia*, on some Polynesian islands, as gradually losing its prongs, increasing its seed size (to a record in the family), and its height to tree size. Advance in growth makes it finally conform to original inhabitants of a forest (see p. 105).

Little difference of opinion can exist on transoceanic immigration in the (recent) Galapagos islands. The loss of dispersability after settlement is demonstrated by the composite genus *Lecocarpus*, which lost its pappus. Secondly it acquired a wing-like bract on its achene after new radiation. The general lack of dispersibility is thus demonstrated as a secondary phenomenon. Little difference of opinion exists on transoceanic immigration to the Galapagos Islands from the continent.

An interesting discussion between scientists on either side of the question may be found in the symposium proceedings edited by Gressitt (1963). Here, van Steenis defended the concept of land bridges against Fosberg, maintaining the idea of rare endemics as relicts. Both authors take as a main basis the "steady state", the permanence of geographic and climatic conditions during the specialization of higher flowering plants in and after the Cretaceous. Continental drift and a major shift of climatic zones are apparently excluded as explanations of their distribution, in contrast to the situation with older life forms.

For a more extended review of van Steenis' views opposing transoceanic dispersal, see his special article defending ancient land bridges (1962). The paper is admittedly somewhat negativistic in its defence. It cuts, in regard to the lack of pappus of Compositae and the largeness of many insular diaspores, the possibilities of gigantism, precinctiveness and derivation from large drift-seeds. In regard to the impossibility of spread and establishment of rain forest plants outside their forests, it neglects the fact that they can follow pioneering nomads. Van Steenis mentions *Gahnia*, *Carex*, etc. as spread over immense areas, yet having no structures for endozoic or epizoic dispersal by birds.

In his mighty monograph of *Nothofagus* (the concept of land bridges has been mitigated meanwhile) the background of van Steenis' aversion is again clear: A very old Malesian-centered genus is spread over much of the Southern hemisphere without apparent means of distant dispersal. Middle Cretaceous fossils in New-Zealand, also fossils in South America and Antarctica are known. A Gondwanaland origin of Fagaceae is indicated as impossible. He finds no explanation for the disjunction with South America and claims a "New Chorology" as necessary. Others found an explanation in early differentiation in Gondwanaland followed by break-up, or even claim early presence in North America (as for other Fagaceae). Though there has been no palynological support until now, they compare the migration with the one of Marsupialia in the Cretaceous, from North America via Gondwana to what is now Australia. *Araucaria*, comparable in recent disjunction and in low dispersability, has fossil representatives in the North. It is more ancient.

A general curiosity in the "tracks" of many distributionists is that these scientists use tracks as the reflection of dynamic, progressive extension, but switch to a static concept of relict-nature as soon as small, disjunct areas are to be considered. When disjuncts are found far from a common centre of origin and without obvious means of dispersal, one asks how they first arrived and looks for a condition changed in some respect. The supposed land bridges are, curiously, mostly described as having one-way traffic.

Further concepts related to ancient land bridges lie too far outside our field to be dealt with here in detail.

Disjunctive distribution not connected with dispersal has been connected with continental drift. This has been accepted for old families present during the Cretaceous in continents before they split apart. Raven and Axelrod (1972) analysed this positively, though also accepting long-distance dispersal in general. Smith (in Meggers et al. 1973), to the contrary, stated in his analysis that angiosperms arrived too late for their distribution to have been seriously affected by continental movements.

The separation of North America and Europe probably started only in the Eocene, thus the distance between them was for a long time less than it is at present. This has been brought into relation with the old puzzle of how some American spp. could occur in Iceland and Norway, not to be explained by mere dispersal. In 1967 Löve and Löve already explained distributions in the Arctic-Alpine flora by drift, followed by local adaptation of species. Theories on the

origin of angiosperms in isolated mountain regions do not comply with early uniform distribution over old, unseparated lowlands.

## 6. Plant Sociology and Dispersal

The term "sociology" is not a very apt description of the study of plant communities, as this deals, even on the botanical side, not with equal "socii" but with competing species. Moreover, it must also include the zoological influences in the biocoenosis, so often neglected in temperate regions.

When dealing with new and rejuvenating vegetation, the student of communities cannot afford to neglect the transport factor. The creation of dunes in Holland is based on the special dispersal methods of *Triticum* (*Agropyron*) *junceum*. After primary wind transport overland to the sea, the fruits can (at least locally) endure further transport by salt water. They are washed ashore and germinate in flood marks rich in debris; they do not die off after a year like *Salsola* and *Cakile* but remain rooted in the rich substrate; then dunes form around them (van Dieren, 1934).

Feekes (1936) studied the succession in a new polder in the Netherlands, stressing for the initial phase (occurring in the region still covered with salty water) next to sedimented seeds in the silt, the importance of "drift", plant complexes carrying with them nonhalophilous diaspores, so that the later-appearing soil was by no means virginal. In the following more or less dry phase the contribution of epizoochory and endozoochory by waterfowl was important. Many migrating thrushes and finches later contributed, after feeding on *Atriplex* and *Suaeda*. Endozoochory of real berries played only a small role in this wet, semihalophilous phase, in an illfitting biotope. His results relating to anemochory have been discussed before (p. 69).

Some cases of inland repopulation have been mentioned before, but we will refrain here from discussing further incidental cases and effectivity of different dispersal systems.

The American school of "ecologists" (mostly sociologists) has always been dynamic, paying much attention to succession and showing some interest in dispersal; as described here, European plant sociologists as a group, however, have seriously neglected the transport factor, minding only the substrates for correlation. Their synecology is mainly descriptive, and so are their succession studies. Feekes apologized that the succession in the polder is not a proper object for theoretical sociological considerations but tried to apply them nevertheless.

The study of agricultural weed communities also offers such difficulties, since they are rather incidental, ever-changing complexes, associations in the literal sense. In a sociological symposium on anthropogenous vegetation (Tüxen, 1966) all reproductive processes, so crucial in this matter, remained undiscussed.

The more experimental researchers in Europe (cf. Knapp, 1967) have paid special attention to measurable factors acting in the vegetative sphere. In the reproductive sphere they have limited their attention, probably rightly, to germination. Perhaps dispersal seems to them too clearly a property of the



individual species, though important in succession. Heimans (1954) tried for years to arouse interest in the transport factor, coining on the side of the habitat the concept of accessibility, which had already been applied in historical plant geography. Its counterpart in plants might be considered too, under the name of "aggressivity". This characteristic has been analyzed for weeds, as discussed in Chapter XI.

One must admit that the role of dispersal is difficult to analyse in a steady ecosystem with constant internal rejuvenation.

For some large-scale, physiognomic communities, unstable invasive, open and stable, closed and dense respectively, such as deserts and rain-forests, dispersal spectra have already been described in the foregoing sections. As my knowledge of "plant sociology" is restricted, I refer readers for the study of dispersal in diverse associations to the discussion of some European papers in pp. 129–132 of Müller (1955). There graphic representation of dispersal classes in associations is to be found.

The main part of Molinier and Müller's study (1938) on the different communities of southern France consists of a comparison between their dispersal spectra, also between the succession stages. Clear differences were found and the connection between aridity and autochory was confirmed.

Salisbury (1942) plotted fruit setting, seed size and output, and the viability of diaspores against habitat conditions, finding interesting correlations to be discussed on p. 120. Dansereau and Lems (1957) felt that a functional analysis of sociological units and succession should also involve coefficients of dispersal types. They tested this on North American plant communities. The results were similar to those of Molinier and Müller. They mixed agents of dispersal, agents of breakoff and presumed morphological adaptations in the naming of types, sometimes deliberately ignoring the fact that a winged diaspore is not necessarily anemochorous. Dansereau and Lems on this basis, proposed the new grouping of diaspores, mentioned here on p. 8. The readily recognizable morphological features were taken as criteria for constructing what they call dispersal spectra in communities. I admit that this procedure is probably justified in their field, but I criticize their terminology and its application (by others) in our field, to the ecology of dispersal as a general process.

A new application (with more recent literature) is the one by Luftensteiner (1979).

## 7. Coordinated Dispersal

We found some traits of co-ordination in the rain-forest, (providing continuity for dispersers, possibly needed later for recolonization) more than in other vegetation, where (at best) parallelism was encountered. In Chapter XI on weeds, we shall find that many weeds are dispersed by human agency to all sites where crop plants are sown. It is worth investigating whether something on the lines of lichens exists in higher plants, where the components can spread together.

The diplochory of some tropical shore plants (see p.97) not only provides additional dispersal inland but also makes life possible for bats and birds. When migrating, these can at the same time bring in other inland plants.

More evidence in this direction it to be expected in parasitic plants, where we found some precision, e.g. in the burying of seeds by ants (*Lathraea*, *Mystroptalon*), in hyperparasitic Loranthaceae reaching their host plant by means of the common disperser (*Dicaeum*). Barquin and Wildpret (1975) saw that from faeces of *Lacerta* (see p. 26) plantlets of a *Cuscuta* arose, next to those of *Plocama*, to be infested. Atsatt (1965) reported coordinated dispersal of the parasite *Orthocarpus* as the diaspores hook in on the pappus fruit of the host (*Hypochoeris*). The combination with an introduced host seems accidental, but is fully effective. If one wishes to see the plants in "ant gardens" as an association, one finds coordination in dispersal in a community, perhaps even among other ant plants.

Feekes (1936) pointed out that tumbleweeds can carry in their complexes many diaspores of other plants from the community, even rather heavy ones.

## VII. Establishment

### A. General

Treating only the transport of diaspores in this book would result in a picture without background, not fully deserving the name of ecology. This has already become clear in the earlier chapters, where a discussion of the nature of diaspores showed, time and again, bonds with later phases of life. A similar situation was found in the time of presentation.

We have to deal here also with the aspect of germination of the diaspores just as is necessary in floral ecology, where processes that start to work after the transport of microspores are found to have been "built in" from the very beginning in the properties of spore and stigma. Such processes have to be put into our picture, the more so because many ecological aspects are neglected in laboratory work on germination. One might say for many diaspores that the destination is built in. Admittedly, diaspore dispersal never attains the exactness which pollination displays in reaching with precision a favourable substrate at the right time; still, we may draw parallels with the matter treated in *The Principles of Pollination Ecology* (Faegri and van der Pijl, 1979). The peaks, already described here, are myrmecochory, Loranthaceae and Dicaeum, and some mechanisms of atelochory centered on germination in a favourable place.

We have already seen that some discussions of recolonization (e.g., those concerning Krakatau) have neglected the suitability of the substrate. On the other hand, many other studies concerned with recolonization after volcanic activity have paid attention almost exclusively to succession in connection with the changing substrate and have neglected dispersal.

On the side of diaspores, the chain to success is the following:

maturation (+ dormancy) → presentation → dispersal (+ after-ripening + protection + longevity) → fixation → germination (+ breaking of dormancy) → establishment (ecesis of Clements, in a certain sense).

I should be noted that this refers to the plant individual. In regard to a plant species, we may speak of establishment only when the individual reproduces itself.

The feed-back of adults, already present, can – as before – be treated here only incidentally. Smith (1975) tried to quantify and to integrate these processes for the invasion into a pine stand of some ornithochores. He also considered predation on seeds as a factor.

## B. Fixation

In anemochores, hairs may finally act as anchors on the substrate (they can easily be transformed into them entirely). We saw this in plumose epiphytes. In desert plants and water plants, the dispersal and fixation functions of burrs are concurrent. The anchoring aspect in desert plants is clear in their myxosporry. The production (after rain) of slime makes the diaspores after desiccation adhere to the temporarily moist and coherent soil, preventing their being blown away afterwards. This adhesion also provides the counterforce needed for penetration of the radicle and the slimy mass may also favour germination. Some authors consider it in other cases as preventing premature germination, e.g. by forming an oxygen barrier. Murbeck (1919) devoted the first part of his study to this phenomenon in the most divergent families; it is best expressed in Cruciferae, Compositae and Labiatae. The drier the climate, the more myxospermy there is. Stopp (1958 b) described the fixation function of myxospermy in South African Acanthaceae. In an extensive general review Grubert (1974) gave details of the layers concerned, adding experiments on supposed ecological effects. For myxosporry in cataracts see p.71.

We saw on pp.73, 78 and 85 that in humid regions and in aquatic plants myxosporry may also be connected with transport. What the effect may be of a myxospermous testa enclosed in a tough pericarp, as in the *Bidens* spp. described by Lhotska (1968), remains to be investigated. Mayer and Poljakoff-Mayber (1963) mention more instances where the mucilage may be released after the splitting of the fruit wall. This occurs in the fruits of the grass *Sporobolus*. According to some observers the slime on the seed means no mere fixation after dropping, considering that the seed may remain sticking to the open caryops on this plant.

In *Prosopis farcata* the slime in desert forms is secreted by gum cavities in the endosperm, when the palisade layer has peeled off (Werker et al., 1973). We already met this (p.78) in some Acanthaceae.

Zohary (1937) distinguished eight types of secretion but expressed doubt as to its ecological significance for fixation, since in Palestine during the dispersal period the soil is sufficiently moist for quick penetration. Stopp (1958) found that, in many desert species of *Oxalis*, a nude embryo is expelled by explosion and is soon (after wetting by dew) enveloped in mucilage from the radicle, which afterwards dries and glues the embryo to the soil. In the slime the radicle develops very fast.

Another method of fixation (especially on loose soil) is the hygroscopic boring action (trypanocarp) by alternation of drying and wetting in *Avena*, *Erodium*, *Stipa*, etc. The stiff barbs serve for arresting. Zohary (1937) described it for forty-eight species and confirmed the result, doubted by some authors, though he was again most specifically interested in its atelochorous aspect. Not all *Erodium* spp. (plumed or not) are efficient drillers, though possessing moving awns. On loamy soil often no penetration occurs at all – linking dispersal and the wanted substrate. Simpson (1952) confirmed the effect of awns in a boring grass



(*Danthonia*) experimentally. Six months after sowing, twelve times as many seedlings were established from awned as from de-awned grains. The effectiveness stands in inverted relation to the effect of the awns for distant dispersal. In the geographic distribution good correlation exists with aridity; this holds true also for Australian and American species of *Erodium*. Many other atelochorous devices, such as geocarpy, provide fixation. Fixation may also determine the right position at germination. We see that establishment promotion is included in the device for dispersal. In drilling grasses such as *Stipa*, *Stipagrostis* etc. foregoing epizoochory and anemochory also provide dispersal.

A transition between trypanocarp (of detached ripe diaspores) and geocarpy (of attached growing fruits) exists in *Trifolium subterraneum* ssp. *brachycalycinum*, where the developing fruiting heads on a thin peduncle are buried by movements of the bristle-like sterile flowers (Morley in Baker and Stebbins, 1965).

### C. Vivipary

This phenomenon, a growing out of the embryo on the mother plant, bridges or oversteps fixation and germination. It may skip both, as it does dormancy. There have been speculations, e.g., by Guppy (1906), on vivipary as a general property of primitive angiosperms, still lacking dormancy, protection and dispersal. The presence of the latter processes in Gymnosperms does not favour this concept. We shall meet vivipary as a derived condition in special habitats, not as a lost general habit, nor as just a strategy in a predictable environment without seasonality (vide the rain forest).

Vivipary is best known from mangrove plants such as *Rhizophora* and *Bruguiera* and is often classed as just barochory. Its function is then presented as a means to implant the seedling directly into the silt: fixation without dispersal. An objection is that at high tide this mechanism is void. One tends to doubt an opinion or observation ascribed to Beebe, that the embryos are dropped at low tide only.

Direct implantation has been doubted. Near Miami Lawrence (1949) saw seedlings underneath mature trees of *Rhizophora mangle*, but they were not erect or bent upwards, nor recently detached. On the contrary La Rue and Muzik (1951) found a considerable percentage of vertically implanted seedlings in a place where tidal action was weak. The roots grow some centimeters per hour and develop side roots within a few hours.

Desert researchers, fascinated by atelochory, may consider the phenomenon as a means to avoid dispersal (near the sea by currents), as Stopp does for the viviparous *Oxalis* just mentioned, where fast germination is an important side effect in a dangerous, almost waterless environment.

On the other hand, vivipary has a clear relation to a water habitat in the cases of the floating embryos described in the section on hydrochory (p. 75). Perhaps in those developed, nude embryos the essence is just superfluity of the

testa, whereas atelochory is there redundant since the embryos float away. In the Araceae *Cryptocoryne ciliaris* (occurring in tidal mud) and *Aglaodorum griffithii* (found in fresh water) there is a real link with vivipary in the floating, further developed embryos. We see real vivipary in some other mangrove plants, e.g., in *Aegiceras* and *Avicennia*, where the seeds germinate in the fruit, which then floats away till the anchors stop dispersal.

In Australia, marine *Amphibolis antarctica* seedlings break free only when 7–10 cm long.

On the dispersal of *Rhizophora* much controversy has existed since the work of Ridley, but we may accept that floating is the rule and that under special circumstances the plantlets can strand, root and erect themselves (Egler, 1948). In agreement with this opinion is the observed young *Rhizophora* vegetation, where all plants seem to have been established simultaneously at a certain distance from old trees. In Java the circular water movement at dead tide with its boring effect on vertical embryos, first described by Egler, has also been observed. The vertical position is also attained after dilution with fresh water.

It has been argued (Joshi, 1933) that implantation of *Rhizophora* has, nevertheless, as in desert plants, a relation with an endangered water balance. It might prevent germination of a vulnerable embryo on the surface of the silt where an extremely high salt concentration is found. In many other halophytes the young seedling is indeed less tolerant than the adult plant. Mayer and Poljakoff-Mayber (1963) demonstrated this for *Atriplex halinus*, an halophyte which (like other ones) is bound to dilution by rain for its germination. (*Pancratium maritimum*, *Cakile maritima* and *Triglochin* are other examples). Indeed, the embryo of *Rhizophora* has a comparatively low osmotic value (about 20 atm, due to sugars) when compared to the mother plant (about 30 atm, due mainly to chloride). The embryo has to receive water by active secretion from the pericarp, which makes the situation indeed vivipary. According to Blume (Rumphia 3) *Nipa* (*Nypa fruticans*, from brackish tidal mud, has a beginning of vivipary. The fruits are not separated until internal germination is far advanced. This has been verified by Tomlinson (1971).

Although in *Cocos* we find development on the tree only in exceptional cases, the beginning vivipary of *Cocos* (p.76) and of the Amaryllidaceae discussed below, also with a water reserve in the seeds, can be considered as promoting fast germination in habitats poor in water. In the latter seeds, dormancy is skipped. So we return to the aspect of lack of usable water on the shore and in the steppe.

Some shore species of *Hymenocallis* have seeds with a thick, watery, vascularized integument. The seeds burst through the pericarp at an early stage and the reclining shaft of the inflorescence deposits them on the ground. Some shore species of *Crinum* have comparable, very large and floating seeds. They are testa-less, originating from reduced ovules that are undifferentiated (here not connected with parasitism). A layer of dead endosperm cells takes over for protection. The seeds germinate without added water. Transference of function from the testa occurs also as the watery endosperm forms the reserve in a convergent way. The same vivipary occurs in some South African *Nerine* species

from steppes. A radicle-like protruding integument is often already visible when the seeds, with their watery, photosynthesizing integument, are liberated. In this light one can consider the statement in Engler-Prantl that the ovary produces bulbils. From the extensive literature I mention only some later papers, such as those by Dutt (in Maheshwari, 1962) and Whitehead and Brown (1940).

Seeds of Loranthaceae, testalese and germinating on nude branches, also have a water reserve against the danger of the substrate drying out. They can develop organs without help of outside water, even when fastened indoors on wood. The succulent vegetative bulbils of *Agave* and *Bryophyllum* also have more connection with fast germination in deserts than with atelochory. Probably they root faster than seeds with distant dispersal. The atelochory is at most a side function. The vivipary of *Sechium edule* (Reiche, 1921), a cucurbitaceous plant from Central America, concerns a normal fruit, well known as a vegetable all over the tropical world. The juicy and slime-containing cucumbers are obviously without inhibiting substances. They let the single seed sprout when it is still enclosed and are planted as such. The sprout in the isolated fruit can reach a great length. This deserves physiological investigation.

In contrast to primitive groups with an undeveloped embryo, grasses have an over-developed one (see Chap. X). This has consequences.

Some bamboos (spp. of *Melocanna* and *Dincholea*) show vivipary, though they are neither desert nor shore plants. Stapf (1904) demonstrated that the nude and, at maturity, endospermless embryo absorbs water from the juicy pericarp.

According to Vaid (1962) most fruits are dropped before germination, but they sprout immediately. Late in the season (when the atmosphere becomes humid) the remaining fruits show vivipary. Regular endozoochory of the large, pearlike fruits is improbable as the embryos possess no (at least no mechanical) protection against being crushed.

There is no fundamental demarcation of this phenomenon from the so-called incidental vivipary of cereals, where normal seeds sprout precociously on the plant as a result of excessive humidity. In some species of *Inga*, this occurs so regularly that the bond with water or aquatic animals comes again to the foreground.

The conclusion on vivipary is, just as for geocarp, that it is a phenomenon serving establishment in a wide range of environments and that it has divergent origins. It may be based just on abolition of protection, desiccation, and the rest period. This is superfluous in water and unwanted during the favourable period in arid regions. The confusion is promoted by some handbooks which do not analyze the functional side and may, like the one by Ulbrich, include false vivipary, which was excluded here on p.12. Some even designate this as true vivipary. Mattfeld (1920) illustrated the confusion and sought to escape by designating fructificative vivipary as "biotechnosis". This term is superfluous and is just a Greek translation of the Latin word "vivipary" ("technosis" = bearing).

## D. Germination

### 1. General Importance

From dispersal we now shift to a field of its own with a rich literature (Mayer and Poljakoff-Mayber, 1963) and later works (Isr. J. Bot. 29). This is not to be summarized here, but we may look over our self-imposed wall to see what grows out of the roots in our field, as explained on pp. 91, 100, 116 and elsewhere (see Chap. X). This with apologies to the reviewer who condemned such "half-hearted excursions into physiology". In fact they concern here not ordinary physiology but (as in much of this book) synphysiology of systems. Ecology of entities means physiology of the higher system. Often physiological research in the laboratory cannot entirely predict results in the community.

Some superficial reconnaissance into this other field seems necessary, because diaspores reflect so much of its characteristics, as became obvious in the foregoing sections. The phase of germination is often the most critical one in the life of plants, and especially so in some communities where the diaspores, as a preparation for the seedlings, must be adapted to meet the special requirements. Went (1949) described how the floristic composition of desert areas in California is determined largely by rapidity of germination in the short periods of rain. The temperature optima for germination in such regions differ strongly in winter and summer annuals. When saying that the germination response determines the distribution range, such investigators overestimate the importance of their field somewhat, just as some old investigators of dispersal and pollination did for theirs.

Koller (1964) has published a fine review article (seventy-seven items) on the survival value of germination-regulating mechanisms. The contribution by Thompson (in Heywood, 1973) reviews new data, including those on genecology. The germination of stranded halophytes only after lowered salinity (p. 178) has the side effect of inhibiting germination during transport.

In aquatic plants, germination deep under water would be unlikely to lead to seedling survival, as Mayer and Poljakoff-Mayber (1974) point out. The requirement of adequate light prevents this, favouring shallow places. However, in most instances of stimulation by light or even special lighting, the ecological function served by the light is not clear. (This does not apply to light as a general condition in competitive germination).

Stebbins (1950) points out that large diaspores in loose desert soil are necessary to make rapid formation of deep roots possible. On the other hand largeness, with a relatively small surface, means difficulty in direct uptake of water. The texture of the surface may act similarly. Here is still another demonstration of the manifold influences on diaspore size, including germination requirements. See also Janzen (1969 b).

In closed communities, the competition factor plays a role in germination, requiring resistance to many factors, and patience. Salisbury (1942) has shown for Britain a relationship between the seed weight of a species and the kind of



habitat or stage in succession where it occurs. Seeds in woodlands are the heaviest, with dispersability having lesser importance. For rain forests this has been pointed out in Chapter VI (for non-epiphytes). Selection there acts somewhat late in older seedlings with so-called advance growth. The case of *Mora*, with its gigantic poisonous seeds, was cited on p.90. Thousands of 1½-m high seedlings have to wait for their opportunity to obtain the full light they now need. *Quercus* and *Castanea* are also at home here but have found a way to escape (p.30).

In both kinds of woodland there are exceptions with smaller seeds (see the left column of Table 2, p. 105 that do not require shadow for germination. Salisbury called them "opportunists", van Steenis (1956) called those in the rain forest "nomads". They are reservists, meeting catastrophes by forming a secondary growth. The "nomads" may persist on the fringes in the climax, rarely surviving as high seed trees (*Pinus merkusii* in Sumatra). Here, too, germination limits can be narrower than those for further growth, so that near their upper limit (determined by germination) some trees grow optimally.

Harper (in Baker and Stebbins, 1965) reported that plants (*Plantago*) introduced into meadows suffered from germination and establishment hazards that were innocuous for adults. The seedlings had to rely on favourable microsites. In deserts the first days after germination can be decisive. For grasses see p. 181. In Argentinian pampas (climatically suitable to tree growth) compact soil favours a closed grass vegetation. Its dense superficial root systems seem to inhibit the establishment from tree seeds, when not assisted.

From this vast field of germination biology, we select a few topics for our purpose.

## 2. Span of Life and Dormancy

Delayed possibility of germination is often roughly indicated as dormancy. Authors often exclude delay through purely environmental factors at release. Such induced dormancy is not always to be differentiated from an innate one when the said induction was a stimulus for lasting inhibition. One might also doubt the innate character when auxiliary layers are decisive (see p.99).

Dormancy (innate or induced) has as a function first to prevent immediate germination, when the circumstances are still temporally favourable but consequently no more so to the ensuing seedling, and second to bridge over the immediately unfavourable circumstances, climatic or biotic.

Innate dormancy may be due to: (1) rudimentary embryos, (2) physiologically immature embryos, (3) impenetrable, resistant seed coats, (4) the presence of inhibiting substances.

The sudden appearance in the soil, after disturbance, of seedlings from seeds buried for years, has long been a puzzle. The foregoing high concentration of CO<sub>2</sub> has been abandoned as the decisive factor. Simple shift to illumination is also not sufficient. Stronger fluctuation of temperature is probable.

Longevity of diaspores must, as we have seen, be in consonance with the way of dispersal. It must also have a connection with the climate and its alternation of seasons. For exact data, I refer to Crocker (1938) and Barton (1961), as well as the latter's contribution to the *Encyclopedia of Plant Physiology*, Vol. 15/2 (Berlin-Heidelberg-New York: Springer 1965).

In the rain forest (see Table 2), the period of possible germination in open air is often over in a few days (this is true also in *Hevea*), always excepting the "nomads". The range in longevity of seeds of "escaped" species of *Quercus* and *Castanea* deserves to be recorded in a table. The seeds of European species are, like beech and walnut, already known to be relatively short-lived. In America black (red) oaks are considered as having dormant acorns, in contrast to white oaks. The nomadic nature of wild *Musa* species is confirmed by the long-lasting dormancy of their seeds (Simmonds, 1959).

Especially in desert regions, the life span of isolated seeds and of complete diaspores of one species may differ greatly, a fact which should not be neglected, as demonstrated in the section on heterodiaspory in Chapter VI.

In sea-dispersed diaspores, where we saw salt as a menace to the embryo, the life span has been the subject of much study by Guppy (see p.76). The case of the lotus (*Nelumbo*) in fresh water is not exceptional. Estimates of the age of "seeds" buried in Japan (and still vital) vary, but point to some centuries. For *Canna* see Sivori (1968). The hoaxes with "pyramid grain" have caused confusion among the public.

Archeologists and geologists have reported living seeds in layers up to 10,000 years old. For *Lupinus arcticus* see Porsild (1967), for *Spergularia* and *Chenopodium* spp. see Ødum (1965).

In cultivated cereals, agriculturists, anxious to grow as many generations in as short a time as possible and in every climate, have for millenia tried to overcome dormancy. One result has been that wild cereals have become a problem by remaining dormant in the field. Weeds have to be versatile in this respect, too.

The anatomical side of innate after-ripening is evident in (? primitive) seeds, where the embryo grows out after detachment as in many Gymnosperms and primitive *Degeneria*. In Ranales this phenomenon occurs in *Magnolia* but persists even in Ranunculaceae, such as *Anemone* and *Ranunculus*. It also occurs elsewhere, as in *Ilex opaca* and *Fraxinus excelsior*.

Sometimes the seed germinates and produces roots, but the epicotyl remains dormant, sometimes awaiting a second chilling. This has been seen in species of *Asarum*, *Paeonia*, *Viburnum*, *Trillium*, *Eranthis*, *Hedera* and *Lilium*. In some Connaraceae, Burseraceae and Leguminosae, dormancy starts after the unfolding of the primary leaves (pseudocotyls). Other innate mechanisms offer intermittent possibility of germination. Impermeability of the seed coat can mask this or override it.

### 3. Influence of Dispersing Agents and Other Stimuli

Inhibiting substances may be present in fleshy and dry diaspores. In deserts, rain often has to wash out the inhibitors which prevent germination after superficial

wetting. The passage through animals can remove inhibition apart from embryo dormancy and influence the seed in other ways, as is known to cultivators. We have found this already (p.47,54) for reptiles, birds and ruminants (see also Ridley, pp. 337–338); passage through the latter is especially needed to counterbalance the presence of an extremely hard coat on the seed. In America this is well known for *Prosopis*. A parallel with the described dependency on turtle passage (p.25) is formed by the suggestion that the lack of trees of a sp. of *Calvaria* on Mauritius, younger than 300 years, is due to the extinction of the dodo. In contrast to present consumers of its drupes this large bird (with stones in its gizzard) could probably abrade the large, very hard and thick kernels, so that at the time these still could germinate naturally. All this means high quality dispersal. One curious case in an aquatic plant, that of a *Potamogeton*, proves that this plant is not purely hydrochorous. Germination proved feasible only when all the factors imitating passage through birds were realized (Lohammar, 1954). I found a large difference in germination time between seeds of *Bixa* with and without aril. Osmaston (1965) reports improvement after passage through bats. For birds see Krefting and Roe (1949).

It seems somewhat over-hasty to indicate such data (as is often done) as proof of co-evolution, but on the other hand it seems wrong (seeing also the works of Janzen) to doubt the advantage of prevention of germination near the mother plant, without animal passage.

The influence of the accompanying dung is a point apart. In the case of *Cucumis humifructus* and the aardvark (p.54), the dung is thought to be important.

Mechanical abrasion of hard seeds during transport over sand and in the sea has been mentioned. The influence of some kind of light has already been discussed as potentially of ecological importance. Seeds of Loranthaceae need light so much that some die in darkness on a further suitable substrate. In sociology it is important not to neglect the possibility that proved correlations of occurrence with light may be based on germination requirements, not on requirements of the adult plant. We have to pass by further triggering of germination by all kinds of stimuli, since this has little relation to dispersal. It should be mentioned that seeds can also inhibit each other (Evenari, 1949 and later), and that leaf litter of one species can prevent the germination of other species both mechanically and chemically (e.g. the case of inhibiting *Brassica nigra* in California). It should also be mentioned that seeds may contain antibiotics against microbes and repellents against insects (Janzen, 1969 b).

Some words on the influence of fire (not always an anthropogenous factor), which is often important to promote germination of hard seeds and gives some tropical species of *Acacia* and *Albizzia* an advantage in burnt-off regions, thus determining the local floristic composition. This influence can act even in an earlier phase, namely on presentation. In Australia the woody, indehiscent (macrobiotic) fruits of some Myrtaceae (*Callistemon* and some species of *Eucalyptus*), many Proteaceae (*Hakea*) and the cones of some Coniferae (*Callitris*, some species of *Pinus*) seem devoid of dispersal for years. After a bush-

fire the fruits open, directly by heat or indirectly by the stopping of the water supply to killed branches. The seeds remain arrested for a short time and then fall in a mass on the open, fertilized soil.

In North America *Pinus contorta*, among others, exhibits a parallel character (serotinous), especially races in regions where fires occur regularly. Fires can also regulate germination by doing away with inhibiting litter. Sometimes charred remains of some dominant species trigger the chemical germination of another one (*Emmenanthe*, a chaparral annual).

In the chaparral of California, the seeds of typical plants (*Rhus*, *Eriodictyon*, *Ceanothus* spp.) are favoured by fire as a natural factor of importance (Sweeney, 1956). "Fireweed" (*Epilobium angustifolium*) appears after forest fires, but only as an anemochorous pioneer, its already fast germination being, moreover, favoured by the light and ash abundantly available in the open places. This although simple nitrophily is absent. Formerly some authors thought that only the already present seeds were stimulated by the fire. The topic of "seed banks" cannot be dealt with in general though we treated it for the rain-forest.

Rangers in the South-West U.S.A. use "prescribed burning" to increase germination of wild food-legumes for game birds.

Much literature, mainly on Australia, has been recorded by Purdie (1977).



## VIII. The Evolution of Dispersal Organs in General

### A. Aims

The organs of dispersal in flowering plants will be discussed here from a special functional angle, namely the shift of functions in spores, seeds and fruits. This approach will once more demonstrate the clash between different functions through the ages. It is essential to start with the pteridophytes, although these have not been discussed in earlier chapters. With all due respect to morphology, which has to work with given preceding structures, I hope to give a more functional background to changes in morphology and to the progression noticeable in diaspores.

Table 3 will be used as the basis of the following considerations. The arrows indicate the shift of the functions.

### B. Isosporous Pteridophytes

Four functions in the generative sphere will be considered here.

The spores carry the function of (i) dispersal and (ii) dormancy (more or less pronounced).

The other mobile phase, that of the gametes, is responsible for the functions of (iii) sexual motility, providing genetic recombination, and (iv) sexual differentiation, coupled with sexual segregation.

In the lower part of the diagram (Table 3), which will be examined later on, the functions will again be found, differently arranged, together with more or less new functions of attraction: viz. (v) attraction for microspore dispersal and deposition and (vi) attraction for dispersal of megasporangia (or seeds).

### C. Heterosporous Pteridophytes with Free Megaspores

In the diagram the functions of dispersal and sexuality come together (partly) in the horizontal tier marked "interphase". Here, the sexual differentiation of the gametes has shifted via the prothallia to the spores. It can be seen that the line of sexual shift crosses the line of dispersal shift, indicating that the haplont served both functions. The differentiation between male and female haplonts may also mean differentiation in dispersal, the one by wind, the other by water.

Table 3. Crosswise shift of localization of generative functions and their conflicts in plants

	Adult diplont	Sporangium	Spores	Haplont	Gametes	Resting young diplont	Fruit
Isoporous fern			Detached - Dispersal - Dormancy		Sexual differentiation - Sexual mobility	×	×
Necessary interphase I			Heterospory	Beginning sexual differentiation Sexual differentiation - Megahaplont dispersal in spore			
Seed fern		Sexual differentiation	Megaspore fixed, loss of dispersal	Megahaplont fixation on mother plant Dispersal? by sarcotesta c.s.		?	?
Pre-angiosperm	Sexual differentiation	- Old megasporangium retained	Distant sexual mobility by microspore			Seed dispersal by sarcotesta Dormancy	×
Interphase II						Seed dispersal disturbed	
Angioovulate	Sexual differentiation - New attraction					- Sarcotesta arilloid Dormancy	Fruit dispersal

This schematic representation is a way to bridge mentally the gap between older isosporous Pteridophytes and the Pteridosperms, apparent after the crosswise shift of functions. How the meeting of functions in the interphase may have been realized in the haplonts is a matter for conjecture.

The evolutionary background of heterospory is usually seen from the sexual angle. Phenotypical heterospory provides less mobile "female" spores, few in number but filled with food, and small, numerous "male" spores, mobile in wind or water. The properties of the megaspore are important for safer and faster germination of prothallus and zygote, whereas the microspores rely for their dispersal on safety in numbers.

This may be the primary background, rather than some differentiation or difference in dispersal, only the microspores spread by wind. In some mosses and in a normal leptosporangiate fern, *Platyzoma*, heterospory has been found independent of differentiation in dispersal, apparently only as an expression of genetical segregation in sexually heterozygous diplonts, leading to genetically determined unisexuality of haplonts.

A first handicap arises in the decreased chance of encounter between gametes of unisexual gametophytes. The other handicap, one frequently overlooked but of interest in present context, is that the enlargement of the female spores means more and more the sacrifice of dispersal to distant sites. The first clash between functions! Warburg (Monsunia I, 1900) long ago pointed out that this situation in *Selaginella* calls for countermeasures. He connected it with the relict nature of diverse species that are confined to small areas. The improved catapulting of the heavy megaspores (some inches) in some species may provide some compensation.

It might be profitable to study the actual dispersal of a simple heterosporous plant of this type. In *Selaginella* there has been a suspicion that, in the rather windless forest habitat of tropical species, dispersal by the wind has been replaced by the scattering of megaspores or embryos by raindrops and rain wash (ombrohydrochory), as elsewhere.

It is remarkable that (as Zimmermann, 1959, notes) other recent heterosporous Pteridophyta (*Isoetes*, *Hydropterides*) also have links with water, which can transport large megaspores, megaprothallia, or still larger organs, and bring microprothallia to them. Meeuse (1961), too, has pointed out this circumstance, which also involves dispersal.

Species of *Isoetes* sometimes even have secondary complications on the reproductive organs, which arouses the suspicion that in ancient times there were connections with animals promoting distant dispersal (cf. p. 23).

In the case of water ferns, there has been some discussion regarding their position in the basal stock of ferns. Their bonds with water concern both dispersal (including the gametophytic phase and the zygotes) and the easy meeting of more or less floating gametophytes for fertilization. This condition may be considered either as a survival of an early sideline in water, or as a later regression to this medium. Water-dispersal of female haplonts may occur inside sporangia or more elaborate organs. The puzzling switch to a more or less

leptosporangiate condition and to a megaprothallium and an embryo situated outside the spore wall should, in this view, be considered as induced secondarily by water life.

The microspores may originally have reached the aquatic, floating megaprothallia by means of the wind, as in recent, newly aquatic plants. Water-dispersal of microspores seems here a specialized sideline due to regression, as it stands outside the mainstream of general progression, where microspores are kept in the air more persistently.

The conclusion is (ecologically speaking) that this water transport most probably evolved early in heterosporous Pteridophytes, before the general dominance of higher sporangia on land plants with enclosed megaprothallia, pollinated by wind-borne microspores and already independent of soil-water for fertilization. A reversal to water ferns in an end line of real Pteridosperms (see Meeuse, 1961) in order to escape from a lack of dispersal possibilities or other factors of extinction is also possible – as shown by a comparison with higher plants returned to water.

To this we may add that their success in survival as ancient forms may have been assisted by secondary methods of dispersal: some of their anchoring and floating contrivances (hooks and slime masses) may also have served for animal transport. The more recent birds can later have extended the areas of dispersal (cf. Ridley). There are even papers pointing to the coupling of their area extension with migration routes of birds and to sporocarps inside birds.

## D. Pteridosperms

When the megaspore and the prothallus remain enclosed in the megasporangium, which in its turn remains attached to the mother plant, sexual differentiation has shifted far to the left in our scheme. There is no longer any real necessity for the female spore to be large, and the special spore wall becomes superfluous although it persists even in higher groups. In most Gymnosperms it is, as a consequence, no longer separated from the surrounding tissue, though Martens found a layer of separating callose in Cycadales. Though seed formation is clearly an ecological, polyphyletic convergence, some a-functionallistic botanists consider the non-separation of walls as primary, as the cause of seed formation (cf. Martens, 1951). Palaeobotanists may decide (for seed-bearing Pteridophytes) whether the causal sequence is thus, or the reverse.

Much attention has been paid to the sexual importance of this change to the seed habit. It frees the gametophyte from soil and water. I found less interest in the literature in organs secreting the water which is still necessary for fertilization.

Still less attention has been paid to the shift of the dispersal function to the right in the scheme – not even by Thomson (1927), in an otherwise profound discussion of the seed habit. This attention will now be paid.



The microspores provide no colonization of new sites. The megaspores lose their dispersal function entirely after their fixation in an attached sporangium.

In the scheme of Table 3, the four functions (I–IV from p. 125) can be seen to be disrupted in a curious way, which results in such a major change that, in my opinion, it required an intermediate phase. Once again, dispersal had to find a way out after being suppressed by sexual functions, which come first in ontogeny and perhaps in importance, especially in ferns. It might be better to say “the processes shifted their limits”, as not only the newer haplontic and diplontic parts are dispersed, but also the old diplontic sporangia, once they have served their sexual purpose. The megasporangium had to provide transport to new sites. Simply rolling away (barochory) is a poor means of transport.

The choice is between dispersal (a) before or (b) after pollination, or (c) after fertilization, although all methods may have been followed together or separately in different groups.

The lack of visible stages of embryogeny in fossil pteridospermous “seeds” is no sure indication of dispersal before fertilization, i.e., dispersal in the gametic phase. Zygotes are tender-walled and small and (as has been ascertained for Gymnosperms) a well-developed prothallium in a dropped, apparently mature, seed is no guarantee of fertilization. When growth in a rain forest is considered, the failure of dispersal and dormancy may have been unimportant, as said before, but elsewhere it must have hindered survival, together with other factors. This seems particularly likely after the changes in climate in Carboniferous times when a shift in location became necessary (postulated in van der Pijl, 1955 a). The sporangium and the later cupula probably involve mechanisms invented to escape from this drawback.

Our difficulties in understanding the transition are not over when we replace ferns as ancestors of the Pteridosperms, or these themselves, as ancestors of the spermatophyta, by some form of the Psilophytales, as long as no mobile megagametophyte with wind pollination has been demonstrated there.

Pteridosperms had become true land plants and, though the megasporangia may have been spread by rain wash and flushed into rivers, a general return to real hydrochory seems improbable. Neither the sporangium nor the cupula seems to be a floating apparatus. The megasporangia seem, from the very beginning, too large for simple wind dispersal.

It is tempting to look toward animal dispersal for the large cupulae, megasporangia, “seeds” or “ovules”, but it is impossible to form a meaningful opinion concerning the possible role of early insects. The situation is, however, different in regard to endozoochory, *in casu*, by means of the early transitions to reptiles on the ground and to fish (for sporangia dropped or flushed into water). The swallowing may first have been an accidental one connected with the swallowing of foliage. The occurrence and moment of shedding seem less important than is usually accepted in phylogenetic considerations, whereas the moment of transportability after internal hardening is therefore underrated. Fossil fecal pellets of some small reptiles have been found, containing remnants of the reproductive organs of Caytoniales.

There must have been an early origin of a parenchymatous, probably fleshy, cover of the sporangia in Pteridosperms and even in those fossil Lycopodiales which show a tendency to the seed habit. The originally sexual functions of sporangial appendages (spore collection or water secretion) may have changed into dispersal functions. A consideration of dispersal lends more meaning to swollen integuments and the like than the vague ideas of mere protection expressed by pure morphologists, who forget to say against what. The existence of a fleshy layer is not consistent with dispersal before pollination, since digestion of the outer layers must have prevented pollination afterwards.

As said before, there is an early differentiation in the cover (perhaps convergently) into at least a juicy outer layer (sarcotesta) and a hard, protective, inner layer (sclerotesta). The protection may be against desiccation, crushing and digestion.

I leave aside here the morphological question of where the fleshy layer is a sporangium wall and where (after repetitive transference of function) it is the cupule of a sorus. The argument of Stebbins (1970) that such a dispersal function is unproved, as no sign of detachment of early seed stages with macrospores (the supposed dispersal units) is irrelevant. The ensuing prothallium then would remain unpollinated. Even lack of detachment after pollination of the prothallium inside the persisting sporangium wall would be no valid argument, considering the cited incidental swallowing together with foliage and the case of *Ullmannia* mentioned on p. 131. So, too, seems his statement that the sporangium wall did not undergo a transference of function from "protection" to dispersal. The fact remains that there is a differentiation between sarcotesta and sclerotesta, continued through Cycadales.

## E. Gymnosperms (or Pre-Angiosperms)

We shall not enter into the discussion about where the limits are to be drawn between sporangium, ovule and seed, but mention the (simplistic) scheme of Emberger. According to this, Cryptogams are dispersed as spores, Prephanerogams as prothallia in ovules, and true Phanerogams as diplontic embryos in real seeds. For a critical discussion of this question, see Martens (1951).

In recent Conifers, one sometimes (still?) finds a sarcotesta (*Podocarpus* and *Cephalotaxus*) or an aril, possibly differentiated from it as organogeny indicates (*Torreya* and *Taxus*), and even spurious fruits with diplontic auxiliary organs – all for animal dispersal and even fragrant in *Cephalotaxus*. In *Podocarpus latifolius* the seed is black and the epimatium underneath is red – a typically ornithochorous combination. In *Pinus*, large dry seeds fall into the synzoochorous ecological niche discussed on p.30, which was later occupied by acorns and nuts. Many species of *Pinus* have small anemochorous seeds, but their wings are accessory organs, not produced by the seed itself. *Juniperus* is still more or less gymnovulate, but already angiospermous in its "berries".

*Ginkgo* has greenish, drupelike ovule-seeds with a faint smell, (stronger after freezing), which fall to the ground. They have a juicy sarcotesta and a hard sclerotesta, which seems a continuation of the pteridospermous condition. The dropping seems connected with dispersal (? at the time by ground-reptiles) not with incidental pollination on the ground, as is often said.

We saw on p.35 that recent Cycads are also mostly endozoochorous. In olden times, dispersal undoubtedly was brought about by the reptiles of the period (saurochory). Most *Gnetum* and *Ephedra* species also have zoochorous diaspores with a juicy chlamys, perhaps a transformed perianth from a simplified flower of higher descent. The cones of *Encephalartos* break down.

Wind and beetles for the flowers, reptiles or fish for the seeds, such was the scene at the time! For this assumption there is factual confirmation. Weigelt (1930) described fossil reptiles from the Zechstein (*Protorosaurus*) with a mass of large, intact gymnosperm seeds in their stomachs. This does not point to destructive feeding. The seeds were all of the same size, obviously collected when mature. Schweitzer (1968) later found them in the coproliths, thus dispersed intact. He thought they might have been eaten together with the cone-scales (of the Upper Permian conifer *Ullmannia*). The scales must have been digested, in contrast to the thick-walled seeds. We may perhaps consider this condition as a parallel to *Juniperus*, leading to replacement of the sarcotesta and to its reduction in later Conifers. Later on the scales became dry. Arboreal life of the animal must be assumed.

Gundersen and Hastings (1944) wrote a popularized account on the interdependence of fossil plants and reptiles. After work of Heintze (1927) and Zazhurilo (1940), Russian botanists also paid special attention to this point.

For large seeds birds became better long-distance (and perhaps higher-quality) dispersers than older reptiles, especially for those on dry land and remaining attached in upper regions. They thus provided better colonization from source areas. On the other hand, one might be inclined to suggest a time gap in the presence of dispersers, viz. between the presence of frugivorous reptiles and that of specialized frugivorous birds in the Cretaceous. This could

**Table 4.** Comparison between dispersal and pollination

	Pterido- sperms	Gymno- sperms	Angiosperms		
			Early	Middle	Late
Dispersal	Reptiles ? Wind	Reptiles → Birds and ? Mammals	Reptiles Birds Mammals	Vertebrates Wind Exozoochory	Vertebrates Wind Exozoochory Autochory Ants
Pollination	Wind	Wind → Beetles	Beetles	Hymenoptera Beetles Wind	Hymenoptera Wind Vertebrates

even be considered as having staggered the dispersal of original angiosperms. Considering the continuity of arillate seeds from gymnosperms to angiosperms, such a concept does not seem convincing. Gymnosperms with attached arboreal zoochorous diaspores seem to have persisted meanwhile, representing, though not clearly, late developments. For the difficulty caused by angiospermy itself see p. 133. For aquatic birds the transition was easy (p. 33).

When the bond between animals and dispersal is compared with the one between animals and pollination, it can be seen that the first and oldest one remained one phase ahead during progression in regard to the status of the animals concerned (Table 4).

## F. Angiosperms

### 1. The Seed

We have already discussed possible traces of the primitive situation in which angiosperms were dispersed by vegetarian reptiles. In some groups (*Inga*, *Durio*, Rosaceae, Ranales), there are still traces, also of a later bifurcation in dispersal.

The continuity of the character of seeds from gymnosperms to angiosperms is not entirely self-evident. In the latter group, the ovules are much more delicate, which may, as well as by the occlusion, be due to the disappearance of the large prothallium. The latter became triggered by pollination, not necessarily a specific one, even in its development of archegonia. In many present gymnosperms too, the ovules grow out and form prothallia or archegonia only after pollination. The advantage of this triggering must have been that an autonomous outgrowth or one after unspecific pollination would have meant a waste, at the most producing the embryoless seeds (with prothallia or swollen integuments) mentioned on p. 136.

In the orchids, with utmost precision in their flowers, the triggering is placed further back, at the outgrowth of the ovules themselves.

Arguing for non-identity remains the fact that angiosperms changed to an apparently different, secondary endosperm, triggered by (more specific and later) double fertilization as a new aspect (perhaps not entirely new). Some authors, therefore, considered it imperative to postulate an intermediate phase with no endosperm at all and the seeds consequently small (cf. Heintze, 1927). For this opinion there is no confirmation, and the acceptance of Heintze's view that families with small, scobiform (i.e. having the appearance of sawdust) seeds are primitive, leads to a strange consequence, e.g. to the idea that Orchidaceae and most saprophytes are ancestral. Takhtajan (1959) accepted the large seed as basic, but I cannot follow him when he considers decrease in size as advantageous in progression because it saves building material. We found many more reasons and also reversals; small and large seeds both have diverse ecological backgrounds! See Jantzen (1969b) and Harper, Lovell and Moore (1970), also p. 120. Predators may exert a selective influence on seed size (as



demonstrated for *Bruchids* in Leguminosae) also on the habitat for germination and on the size and methods of the transporters. I wonder if anything is gained by explaining small, reduced seeds as “neoteny”.

The swelling of the integument with food synchronous with the embryo may be temporal, serving for a “Nährzone” to be consumed later by the embryo. It may also be lasting.

The general primitivity of large seeds (megaspermy) has been pointed out by Corner (1949, 1953). It is one of the valuable aspects of his “Durian Theory”, to be discussed later.

Internal morphology of seeds cannot be dealt with here in detail.

Corner (1976) published a grand, illustrated book on (mostly tropical) seeds, describing their testas and drawing taxonomical-phylogenetical conclusions. Whereas others (see above) consider seed characters in a group just as liable to ecological transformation as are fruits, Corner refutes this in general for his subject. We shall not distinguish here between testa and tegmen. Some systems on the relations in size of seed-components do exist. We saw on p. 122 something of this variation. The embryo can also become a group of undifferentiated cells by reduction in parasites and saprophytes. It can, on the other hand, become an enclosed complete seedling with leaves (*Impatiens*, Gramineae).

## 2. The Seed Escaped from Angiospermy

The further development of the sarcotesta seed can be followed in angiovulates (so-called angiosperms), which enveloped their ovules in what will here be called carpels. Broadly speaking, this envelopment is of a sexual nature, since it provides protection against side effects of pollinating beetles, protection against unwanted pollen by a kind of sieve (the stigma), germination and collection of pollen at special places, and so on. It has been sufficiently discussed before (among others by van der Pijl, 1960/61). I shall not, therefore, pursue this sexual aspect now, noting only that its structural mechanisms were interpolated between ovule and seed maturation.

The term “angiosperms” seems incorrect, as it is not the seeds but only the ovules that are concerned in the sexual change in pollination. Seeds were only handicapped by the envelopment and, as will be seen, originally even withdrew immediately from it in many cases. Their inherited dispersal scheme, biotic or abiotic, was again disturbed by the “sexual” process, so that the existence of an unbalanced intermediate phase should once more be postulated, this time between “gymnosperms” and “angiosperms”. Secondary mechanisms became necessary for dehiscence of the envelope and exposure of edible and other seeds, later for transfer of attraction, and so on.

The terms Cryptogames and Phanerogames should be applied in reverse order as ferns have open sex organs whereas seed plants have hidden ones.

The handicap in dispersal in the first angiovulates (see *Degeneria* on p. 135) may again explain, in part, their extinction. Later on, however, when real angiospermy had conquered the initial difficulties, the pluriformity of structures

and methods for dissemination must have contributed to strong differentiation and to the success of the group in a new world with new dispersers.

Sexual difficulties may also have handicapped the first angiosperms. The flowers had to find a niche in a biotic environment devoid of regular flower visitors. They could contact (and partly deceive) some beetles, but the bond was strongly synecological and vulnerable, bound to the environment as a whole, with irregular pollination, — until real flower visitors or reliable, stable connections of another kind had developed (see the discussion of *Ficus*, p. 148).

Maintaining the classical view on at least some of the ancestors of Angiosperms, we must now consider possible means of escape from the menace to dispersal caused by the closing up of carpels.

One means may have been early one-seededness by reduction concurrent with angiospermy, so that in the as-yet indehiscent fruit the carpel was incorporated into the seed. This is possibly the situation in primitive Calycanthaceae and some Monimiaceae, not monovulous by anemophily. There the hypanthium, however, provided a hip, which initially was useful in pollination (it is also present in male flowers), but was utilized for attracting dispersing animals. Originally, the latter swallowed the whole. In those Monimiaceae, this is still clear; the hypanthium there even dehisces like a fruit, though other structures may help in spreading the seedlike fruitlets. In *Calycanthus*, parts of the indehiscent, juicy hip may nowadays be taken (? with fruitlets) by birds (according to Dr. J. W. Hardin, Raleigh) but the achenes are then not yet ripe. He considers the dried-out, untouched hip, still containing the fruitlets, as the mature "pseudocarp", which can be removed by squirrels.

These groups can be considered as being without juicy-fruited or many-seeded direct angiospermous ancestors; the sarcotesta and its derivatives were immediately suppressed. If the new, acarpellate concept for these groups were to be accepted, the clear relationship with other Polycarpicae would become strained.

Corner (1964, p. 212) considered one-seededness as a more or less orthogenetic, autonomous continuation of single-sporedness in the megasporangium and further reductions into singleness. Following this line of thought, one might also see it in Composites as an autonomous feedback regulation of each fruit into a functional seed following integration after increase of flower number in the capitulum. Others see the connection in reverse: flower number was increased to augment the number of fruits when these had become one-seeded. Both concepts ignore trends towards reduction in numbers in some lines. However, with reference to the monovuly discussed before, it seems necessary to point out that this change must have had a more realistic background, and that it is connected with too many ecological sources of pressure to be treated so simply. Here again, monospermy seems a consequence of the constant clash between the function of pollination and dispersal.

Though the application of Dollo's Law on plants cannot be so strict (see p. 146) one wonders at the ease with which some authors allow the disappearance of ovaries and reappearance of ovules in evolution to support hypotheses on the

regulation of seed number to seasonality etc. On the other hand – why could an inhibition on ovule production in the placenta not be annihilated (cf. stamens)?

Most Polycarpicae (despite recent attacks still to be considered as primitive) maintained some form of sarcotesta (see p. 136) and polyspermy (see p. 19).

I see no primary escape in Cyperaceae, where both anemophily of the flowers and hydrochory of the fruits seem to have contributed to secondary one-seededness. One-seededness of this latter kind by itself provides no support for a presumed acarpellate origin. In general, it should not be thrown in with its early, primary counterpart, as is likely to happen in statistical (numerical) treatments. The three styles plead against acarpelly.

Another condition of escape from angiospermy still occurs in simple Angiosperms: the now superfluous covers of “carpels” are dropped or made to burst by the ovules as soon as these start to develop into seeds. On the other hand, the presence of this condition in certain families may prove their primitive nature. Here, too, the concept “fruit” does not yet seem to be applicable to the matured ovary, still lacking complete physiological integration of components. We find here angiovulates that are still gymnospermous whereas many gymnovulates are, in fact, angiospermous.

When considered from a physiological point of view, this condition might also be termed primitive: the transmission of building materials and auxins to the postfloral carpel parts adjacent to the remaining placentas had not yet been perfected when their role in producing megasporangia was fulfilled – as is the rule in organs producing microsporangia.

Such secondarily gymnospermous forms produce large, naked, coloured, berrylike, ornithochorous sarcotesta seeds. Perhaps the definition “angiovulate, not yet angiospermous” is better. Such seeds are found in Liliaceae (Mondoideae), Berberidaceae (*Caulophyllum*), Violaceae (*Decorsella* or *Gymnorinorea*; not ornithochorous are those on the open carpels of *Anchietea*). In Dioncophyllaceae (close to the Flacourtiaceae) the nude seeds are not ornithochorous. In some Celastraceae, the superfluous pericarp is simply thrown off later in the life of the fruit. *Vancouveria* (Berberidaceae) has early dehiscence, exposing young seeds with the sarcotesta developing into an elaiosome.

### 3. The Sarcotesta Maintained in Conventional Fruits

The polycarpiceous relic *Degeneria* has, though the closure of the carpel is incomplete, no efficient dehiscence mechanism in its fruit, and the juicy, reddish seeds (with sarcotesta) usually are liberated only when the fruit decays on the ground (cf. *Durio* and *Inga*). Even Corner (1976) acknowledges the sarcotesta here.

In certain Sterculiaceae it is found, by way of a transition to what may be called a real fruit with angiospermy and dehiscence, that the carpels which have already fused before anthesis split apart and often also open up shortly after pollination. Is the whole (an etaerio) a fruit or not? Ecologically, the open carpels form an escape from angiospermy. They expose the naked, ornithochorous

sarcotesta seeds. This seems to be the basic condition in the family, from which the again separated, but closed carpels of *Cola* (with sarcotesta-seeds) and the permanently syncarpous, indehiscent and fleshy pod of *Theobroma* are derived; the attraction, in the latter case, resides in a special pulp underneath the pericarp and around the seeds (see Ridley). Cheesman (1927) and others have proved that the pulp is a sarcotesta formed from the outer integument.

A parallel temporary fusion of styles (and sometimes of carpel parts) for centralized pollination, with separation and splitting up after it, is well known in some Rutaceae and Simarubaceae. (For palms see p. 137.) This is distinct from the normal syncarpy, which involves in some Polycarpicae only the basal parts.

Many simple Polycarpicae in the tropics have follicles which reopen late without benefit of special structures: often passively by pressure from within, or by disintegration (*Talauma* spp.). In *Magnolia*, secondary, active dehiscence occurs along the "midrib". Related *Kmeria* still has dorsal and ventral dehiscence. When the fruitlets are addressed to the axis, opening along the ventral suture seems adverse to dispersal. Also in comparable *Xylopia* the dehiscence shifts to the dorsal side. The organ, now really a classical fruit, still exposes the old vascularized coloured sarcotesta (also in *Michelia*). Zimmermann (1959) is against the supposed primitivity of *Magnolia* and similar genera and denies that the seeds are simple because, among other things, they have such special, long funicles. In point of fact, there are no funicles at all. The thread from which they hang consists of uncoiled spirally thickened vessel elements from the raphe, as has been known for a long time.

The same condition of secondarily exposed sarcotestas is found in other Polycarpicae, as in some species of Winteraceae, and Dilleniaceae, Bixaceae, Violaceae, Annonaceae (*Xylopia*), some Nymphaeaceae (*Euryale*), as well as in higher groups to be described later.

Elsewhere (van der Pijl, 1955 a), I mentioned the phylogenetical significance of magnolia-like seeds, not knowing that Zazhurilo (1940) had already stressed the link between *Magnolia* and Gymnosperms, and with saurochory, citing Heintze.

In the derived, temperate Polycarpicae (Ranunculaceae), more conventional forms of fruits and seeds have developed. Perhaps the elaiosome of *Helleborus* spp. and the corky body on *Caltha* are remnants of a sarcotesta. The recently separated family Paoniaceae still has beautiful ornithochory on the old basis. Often the opening follicles are still alive and thus show anthocyanins which lend colour to the attractive red valves, as these do to the seeds with their contrasting blue sarcotesta. Sometimes (see Fig. 3) there are special red, sterile seeds indicated as "show-seeds" (Mildbraed, 1964) "Lure seeds" is perhaps better. Dispersal by birds has been observed for species of *Magnolia*, *Sterculia* and *Paeonia*, even when the sarcotesta has become very thin.

In the sterile seeds, consisting of a sarcotesta only, there is again a strong affinity to Gymnosperms. In *Ginkgo*, *Cycas*, *Podocarpus* and *Encephalartos*, similar sterile seeds containing endosperm only occur when foreign pollen reaches the ovule (van der Pijl, 1955 a, and Martens, 1951). Swelling of integuments is there,



obviously, independent of fertilization of the egg cell or of the further development of the embryo (as in empty seeds of pines and firs after hybridization) – a phenomenon worthy of study by fruit physiologists. The many fleshy but sterile seeds of *Degeneria* may be explained provisionally in a comparable way, by independence of the testa.

In some higher (parthenocarpous) fruits the coats of empty seeds have been said to swell by induction from the pericarp by means of a hormonal substance. The relative independence of the seed coat is not astonishing as it is of purely maternal origin.

In some Euphorbiaceae, Meliaceae, Flacourtiaceae, Sapindaceae and Palmae the thick sarcotesta is the edible part of popular table fruits (van der Pijl, 1955 a, 1957 b). In representatives where the sarcotesta became dry the typical outer vascularization might remain.

Among Monocotyledones, one finds large sarcotesta seeds (eaten by man) covered by a thin, dry, finally bursting pericarp in some palms like *Zalacca* (*Salacca*) and *Calamus* (see pp. 26 and 46). For *Salacca* this was confirmed by van Heel (1977 b). I tend to ascribe this to primitivity, though the ovaries are syncarpous. Palm-taxonomists stick to apocarpy as primitive here also. Some apocarpous spp. (*Rhapis*, *Thrinax*, *Trachycarpus*) indeed show a trace of an aril, perhaps just an obturator. The carpology (development of a juicy pericarp with a hard endocarp) must have suppressed sarcotesta and aril in groups that seem farther removed than *Zalacca* from rhizomatose, branched, herbaceous, hygrophytic ancestors.

The condition in *Zalacca* seems unfavourable to the thesis of Meeuse (1966), which considers palm fruits as “synspermia”, fusion products of monovulate, cupulate and acarpellate seed fruits. If, however, a juicy, arilloid sarcotesta is the homologue of a cupule, what can the pericarp be other than a carpel?

The often present septal nectaries seem to make palm ovaries conform to those of liliales – and are basically syncarpous. When we hold on to their apocarpy as basic, the nectaries must have arisen *de novo*, from a situation with nectar on the outer walls of the free carpels. This is indeed present, also in *Trachycarpus*. The ovary in some of the *Livistona* alliance would fit into this concept, being a copy of some Rutaceae, with the carpels free but the stigmas united. The question remains: progression to or regression from syncarpy? Nectar before or after cantharophily?

Some basic Liliiflores (especially Melanthioideae, such as *Littonia* and *Gloriosa*) have exposure of berry seeds. Others (e.g. *Polygonatum* and *Majanthemum*) have the sarcotesta combined with a juicy pericarp (Pohl, 1922, and Kraus, 1949). The descriptive study of seeds in Liliiflores by Huber (1969) contains more cases of free sarcotestas (*Bomarea*) and of sarcotestas fused with a pericarp pulp (*Convallaria*, *Smilax*, *Rhipogonium*, many Asparagoideae, etc.). The sarcotesta is here considered as neotenic and rejected as primitive. Though a hard inner integument is described for such cases, the (very European) argument used is that in a juicy testa protection would originally be absent. For *Hymenocallis* see p. 118.

In the genus *Paris* real berries occur, but also dry, dehiscent fruits with sarcotesta seeds. In Himalayan *P. polyphylla* the latter are red and sweet, eaten even

by man. The difference with nude-seeded Mondoideae is just one of time. Among Iridaceae, South African *Lapeyrouisia*, the well-known temperate *Iris foetidissima* and the tropical *Belamcanda* expose berry seeds, with ornithochory in some *Antholyza* species expressed by vivid colours of valves and seeds. In some species of *Iris*, seeds continue to grow juicy and green even when uncovered artificially at an early stage; this shows that angiospermy is not essential.

The Leguminosae, in their more primitive representatives, also have exposed sarcotesta seeds. They will be treated separately in Chapter IX.

Of course, one could also explain all these cases of a sarcotesta as adaptive convergence, without assuming genetic links with Gymnosperms. However, in my opinion the common roots emerging from basic stock are clear. Absence in ancient Hamamelidae may repose on anemochorous reduction (cf. *Liriodendron*). See also p. 134.

The cases treated in this chapter belong to: Magnoliaceae, Annonaceae, Winteraceae, Degeneriaceae, Dilleniaceae, Paeoniaceae, Berberidaceae, Flacourtiaceae, Euphorbiaceae, Meliaceae, Sapindaceae, Leguminosae, Sterculiaceae, Bixaceae and Violaceae. Further examples are provided by the monocotyledonous Liliaceae, Iridaceae and Palmae (Lepidocaryoideae). A reversal of a hard testa with specialized palisade tissue to a parenchymatous testa seems less probable. One might try this explanation for the isolated cases of *Oxalis* (derived from a mucilaginous epidermis?) and the tomato, where this is really the case. *Ribes* (see p. 143) seems comparable – slimy seeds inside a pericarp – fruit may mechanically facilitate being ingested, even involuntarily. In reference to critical remarks on failing homology of sarcotestas I wish to point out that I refer to the functional device as such. Its homology or histogenetical origin may be as varied as reported for palisade, mucilage, and colour layers of the seed and the sarcotesta-layer of gymnosperms.

#### 4. Arilloids

Further development in primitive fruits will be followed from the viewpoint of functional ecology. The seed coat becomes more protective, dry and hard. For the layers involved and for anatomical details I refer to anatomical handbooks. A high content of minerals is often partly due to crystals. Though these occur also in plants that are otherwise free of them, the crystals may also be due simply to excretion of metabolic side products.

In the rain forest, the seeds of *Magnolia* and the like soon lose their power of germination, a weakness which seems unimportant there for climax forms. For other plants it obviously became important to separate the two functions of attraction and hardness; these should no longer be manifest in two layers as before, but in two parts side by side. Then the juicy part can, moreover, be more easily separated after the transport.

This splitting of functions is reflected in local differentiation of the integument, with the larger part hard and dry, the smaller part juicy and a

remnant of the total sarcotesta. Baillon called such an appendage a localized aril. I prefer to call the juicy part an arilloid. The true aril seems an end product, not a starting point.

This is precisely the field treated by Corner (1949, 1953) in his *Durian Theory*: Modern fruits can be traced back to the fleshy red follicle with many large, arillate, non-dormant seeds. He uses the term aril very loosely, more in an ecological sense, for everything juicy near the seed, using only incidentally (for placental appendages) a morphological criterion. When meeting morphological discrepancies he rather freely invokes a process indicated by him as “transference of function” (see p. 145) defying homology.

It has sometimes been necessary for me to refer in a critical way to Corner. With all due respect for his prophetic vision of the “arillate” fruit as primary, I merely want to take away fringes that hinder insight into the very valuable nucleus. I shall also use a more ecological approach, and in order to provide balance I will try to give the concept more of a head in front (somewhat reptilian since we have to deal with the sarcotesta) and a tail behind (the pulpa).

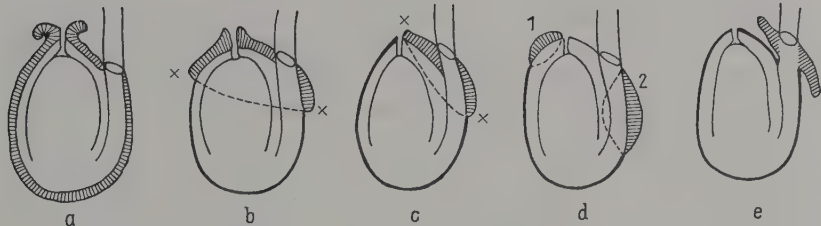
Homology of components in condensed, small ovules (of uncertain homology themselves) is difficult to ascertain. Nevertheless we should not override morphology entirely with arils creeping suddenly into the most different organs. Achenes, though acting as such, are not seeds.

Arilloid outgrowths on or near the seed can be found in four classical locations. Thus we may find (see Fig. 24):

- i) a small swelling on the raphe, a strophiole;
- ii) a small swelling near the micropyle, a caruncle;
- iii) an encircling structure around the exostome of the micropyle, an arillode, sometimes called false aril or exostome-aril;
- iv) a true aril, near the top of the funicle and thus around and next to the seed proper, by some indicated as a funicular aril.

We shall see, however, that combinations are frequent.

The last condition is often hard to distinguish from a diffuse swelling of the free funicle part (in species of *Cereus*, *Acacia*, *Fumariaceae*), a condition which may often be considered not as arilloid but as an incidental adaptive structure



**Fig. 25.** Some arilloids in anatropous ovules as transitions from sarcotesta **a** to aril **e**, via complete arillode **b** and partial arillode **c**. In **d2** a strophiole, in **d1** a caruncle. Integuments simplified, fleshy parts striped, outline on surface dotted, hilum as an ellipse (x-x)

(see Figs. 4 and 5), especially when the whole is long and wound around the seed (contributing to the pulpi-ness of the fruit in Cactaceae), or when the swelling lies at a certain distance from the seed. This occurs in *Labichea* (Caesalpinioideae).

For a modern, critical study of seed appendages see Kapil et al. (1980).

According to our view, the aril is the most derived structure, with complete separation of the functions of hardness and juiciness. According to the classical compilation of Pfeiffer (1891), most arilloids belong to type iii) and do not represent a real aril. I shall not treat the four classes separately here, as they have, naturally, too many links and often alternate within groups. As mentioned, arilloids arise in groups with the sarcotesta basic. Leenhouts (1958) accepted derivation from the sarcotesta in the Connaraceae, so near to the Leguminosae. I argued for such a deviation in Sapindaceae (van der Pijl, 1957 a), as shown in Fig. 25. Other instances of sarcotestas in ariloid groups presented by Corner (1976) are in *Trichilia* and *Aglaia* (in Meliaceae), and *Salacia* (in Celastraceae), some of which are mentioned on p. 24. He considered, however, the sarcotesta of *Nephelium* (Sapindaceae), though firmly attached to the seed, as a far from basic structure.

In the tropics, arilloids are frequent in many families. Corner (1953) has given us a list of so-called arils in 67 families, naturally incomplete but at the same time somewhat overinclusive. The list of the dicotyledones contains, as Corner remarks, the lower families. It is obvious to me that this rests on the older sarcotesta basis, as Fig. 25 suggests. Included are many Polycarpiceae such as Annonaceae, Myristicaceae, Berberidaceae, Dilleniaceae, Nymphaeaceae, Aristolochiaceae and Flacourtiaceae, but also some examples from other parts of the system, Sterculiaceae, Papaveraceae, Cappariaceae, Amaranthaceae, Sapindaceae, Celastraceae, Polygalaceae, Bombacaceae, Violaceae, Connaraceae, Lecythidaceae, Leguminosae, Rutaceae (see p. 142) and Meliaceae. Though their aril is questionable, the Saxifragaceae may be added (*Ribes*) (cf. Kraus, 1949, and Pohl, 1922), and also the Crossosomataceae.

"Arils" are even mentioned in the list for some sympetalous families such as Primulaceae, Hydrophyllaceae (see, however, the section on myrmecochory on p. 57), and tentatively for some Rubiaceae and Apocynaceae, where, however, the soft mass is of a later convergent, placental or endocarpal origin (see the discussion of "pulpa" below, p. 143). Corner (1976) later indicated it as a placental aril. The *Acacia* of Fig. 4 should, accordingly, have a funicular aril.

I objected with a suggestion that the assumed presence of an "aril" in the genus *Siparuna* (Monimiaceae) is due to a confusion of the fruitlet with a seed. Kuhlmann and Kühn (1947) described an outgrowth from the receptacle around the fruitlets, acting as an aril. Later (1976) Corner compromised by calling it a carpellary aril. Now, of course, transference of function exists, but it seems too daring to indicate, in this way, a cherry as a floral aril or a fig as a pseudanthial aril. For the Hydrophyllaceae from the list see p. 57 under *Nemophila*. Finally all arils of Metachlamydeae seem untrue. For *Primula* see p. 57.

The absence of Amentiferae is curious. Though some authors consider their anemophily and their simple flowers as basic in angiosperms, their fruits are very derived. Even the one with the simplest fruit, the *Salix* in Corner's list, should be



deleted since Takeda (1936) has proved the placental origin of the hair tuft. Its *Dichorisandra* (Commelinaceae) has no aril but a sarcotesta (Rohweder, 1969).

The seed-fringe in Asclepiadaceae is sometimes considered as an arillode, which seems exceptional in such a "terminal" family. Now seed-hairs occur in all kinds of higher anemochorous seeds. In the Asclepiadaceae they arise from the micropylar rim but also from the chalazal end of the seed, so that homology with an arillode is improbable.

Arilloids are found in many Monocotyledones, from Liliaceae to Zingiberaceae. Corner (1953) has commented on their absence in Helobiae, so primitive in other aspects and so much like Polycarpicae. Perhaps there is a remnant in some seeds that are liberated, like those of *Aponogeton* (soft, dehiscent testa) or *Hydrocharis* (the slime-hairs around seeds).

Sporne (1954), used the character "seed arillate" as a primitive one in his comparative statistical treatment of the evolutionary level of dicotyledonous families, later revised from time to time. He assigned the lowest advancement index to the Magnoliaceae (curiously not in Corner's list). The typical arilloids are found in families below the 50% advancement index.

To return to ecology: generally speaking arilloid structures are connected with ornithochory on a somewhat higher basis than the sarcotesta, with better dormancy in dry regions.

In some large fruits (which cannot be swallowed whole) the arilloid is eaten by man, who has taken over from monkeys and bats.

In temperate regions, botanists (including antiteleological ones such as Goebel) have often misjudged arilloids in the past, ascribing to them only the role of internal splitting of the pericarp by their swelling or (when situated next to the placenta) as seed disjunctors. In some cases (i.e. Euphorbiaceae) these functions may prevail. In some Marantaceae the arilloids change into springy horns, propelling the seed; in *Phrynium* such change has led to myrmecochory. The aril may serve other secondary functions; in *Nymphaea*, e.g. it makes for hydrochory of loose seeds. In some Connaraceae and Meliaceae it acts as a funicle. Though overgeneralization is dangerous, Corner (1954) suggested it was probable that some anemochorous seed-wings are derived from arilloids in some capsular Sterculiaceae, Meliaceae, Bombacaceae and Celastraceae. They may even be derived immediately from the sarcotesta, as in some Leguminosae.

Many arillodes on anatropous ovules arise from the combination of an exostome arillode with an aril from the hilar region. Then a double circle (figure eight) is the primordial phase. Is there coalescence of separate primordia of organs? For a *Trichilia* sp. (Meliaceae) Corner (1976) described a compound aril, comprising also the arils of five sterile ovules plus a fleshy columella.

Because of their concurrence, there has been some doubt whether the difference between arillode and aril is significant. The aril is basal, the arillode terminal; the aril can overgrow the micropyle, whereas the arillode spares it in its centre. The aril is narrowly attached at the hilum next to the micropyle, the arillode is broadly attached on the seed itself and leaves (after detachment) a broad scar, the false hilum or pseudohilum of *Euonymus* and *Durio*.

A teratological observation seems to favour the idea of separate organs. For *Hitchenia caulina* (Zingiberaceae), Panchaksharappa (in Maheshwari, 1962) describes how the combined aril-arillode of normal, anatropous ovules changed into separate rings in abnormal, atropous ovules, one ring being found around the micropyle and one around the funicle top.

For a morphological background of micropylar outgrowths, one might point to the lobed inner or outer integuments found in some Pteridosperms, Juglandaceae, Flacourtiaceae, Berberidaceae, Hernandiaceae and Sterculiaceae (van Heel, 1977 a). The surface of cells in this region may differ from the rest.

How dangerous it is not to distinguish between aril and arillode is proved by the study of Camp and Hubbard (1963), who tried to homologize the vascularized "aril" of *Myristica* with the cupule of a Pteridosperm. It is, however, essentially not basal and not a true aril since it originates around the hilum as well as the micropyle. The vascularization seems, as in sarcotestas, of physiological significance only (see p.17).

In the literature (Maheshwari, 1963), "obturators" from the outer integument are mentioned for *Coleonema* and all Pilocarpaceae (Rutaceae) and *Rhus mysurensis* (Anacardiaceae). As these organs develop after fertilization, the term "obturator" seems better replaced by "arilloid". Real obturators, guiding pollen tubes, arise early from diverse parts, often from the funicle, and are disorganized after fertilization. This occurs also in higher families. Rarely persisting arilloids arise before fertilization, so that (including in Combretaceae and comparable families) confusion with an obturator is possible. In *Ricinus* and other Euphorbiaceae (with a functional arilloid) this also occurs. The outgrowth meets the obturator. The longitudinal outgrowth of an integument (here n.b. the inner one) of *Leucosyce*, *Canacomyrica* and *Engelhardia*, discussed as an important relic (? expanded ovular stigma), may also be an obturator, as are nucellar beaks of *Codiaeum*. See Meeuse (1966).

I shall let morphological discussion of this kind rest and will devote some more space to the Durian Theory. On p. 83 we discussed Corner's views, not those on tree structure and leaves, but those of spininess, which apparently impressed him so much that he took as a type the durian (*Durio*) instead of his primeval "arillate red lantern fruits". Corner's ideas were also reviewed critically by Parkin (1953). I see that Corner does start with *Sterculia* in his more recent book (1964). The durian (see p. 18 and 54) has no true aril but a combined aril-arillode, as is obvious from the gigantic pseudohilum on the seed. Its dehiscence is not of the primitive *Sterculia* type.

I repeat that Corner's vision of fruits is, justifiably, tropically centered and basically correct. In my opinion, however, he did not begin at the beginning, neglecting the connection with Gymnosperms, which he sees as non-existent.

In later papers Corner (1953) dismisses the argument (cf. van der Pijl, 1955 a, 1956) that the sarcotesta is fundamental and considers it as derived, viz. as a coalescence of aril and seed (even for *Gloriosa* and *Magnolia*) or simply as a case of "transference of function of the aril".

The sarcotesta was, long before, considered to be a conrescent aril. As regards the two families studied by me, the Leguminosae and Sapindaceae (van der Pijl, 1956, 1957 a), anatomy and ontogeny do not sustain this notion.

One of Corner's arguments was that the assumption that the sarcotesta is fundamental would lead to the conclusion that the family Euphorbiaceae is more primitive than is actually the case, and he consequently left it, too, out of his list of arillate families. Sporne (1954) placed it low on his list. We met the family in the basic group discussed on p.27.

Another argument was that the possible presence of a primary sarcotesta in Leguminosae must be denied because, if it were present, the strongly differentiated palisade testa would have gone back to a parenchymatous condition. We have seen, however, that it is present (see also p. 151).

In temperate regions the arilloids are almost exclusively (except in *Ribes* and Celastraceae) represented by the small caruncle and strophiole as elaiosomes. The presence of oil is far from new in arilloids. A long list of cases comprises even temperate *Euonymus* spp. with ornithochory. The link with ants is, as already said on p.55, a relatively new one, still in the process of being developed and acting convergently; in most cases, though, it has clearly evolved from the sarcotesta and arilloids. In such Polygalaceae and Papaveraceae (*Chelidonium* and *Macleaya*) this evolution seems a reduction from the large, red ornithochorous arilloids of tropical forms, in *Polygala* and *Bocconia* respectively. In *Scilla* spp. the elaiosome is exostomal.

The presence of an elaiosome (often formed de novo on seeds) in some Caryophyllaceae (species of *Moehringia*) does not prove their arillate character (see list of Corner, 1953). It is funicular in origin. In myrmecochorous *Carex* spp. it develops on the utriculus (cf. *Scleria* on p.44 for this "aril"). For *Lamium* and *Centaurea* (with "aril" on the fruit) see p.57.

## 5. Pulpa

In accordance with Corner and Parkin, a further eco-morphological progression can be seen in the displacement of seed-coat activity to a more outward layer. In transitional cases this is not to the whole or outer pericarp but to a special outgrowth from the endocarp, its inner layer. The outgrowth, the so-called pulpa, penetrates between the seeds, thus forming a reminiscence or repetition of arilloids, within the tough protective outer pericarp. Thus the protective and attractive layers are again kept apart, with the attraction remaining internal, according to the old scheme. Dehiscence could remain as it was. Support for this concept is to be found in the fact that in some families arilloids and pulpa occur in one fruit or in alternate species (Musaceae, Liliaceae, Marantaceae, Flacourtiaceae, Guttiferae, Sapindaceae and some Annonaceae, such as *Xylopia* and *Artabotrys*). Even some Winteraceae possess a pulpa. In some Guttiferae (*Garcinia*, *Symphonia*) pulpa and sarcotesta together form the edible layer, and in *Ribes*, pericarp, pulpa, and aril. The genus *Pithecellobium* (Leguminosae) has them all, distributed over various species.

What the taxonomic literature, however, mentions as pulpa is a chaotic mass, awaiting ontogenetic investigation. This is especially the case in Flacourtiaceae, Meliaceae, Pittosporaceae and Marantaceae, which all tend to arilloids. As early as 1874, Bentham pointed out this confusion in his revision of the Mimosoideae. Some Flacourtiaceae were studied by van Heel (1977 a). A juicy sarcotesta was found in *Caloncola* and *Camptostylus*, a thin or dry one in *Oncoba* and *Lindackeria* with placental pulp or arilloid around it. These alternate within the family.

Some cases of a pulpa were, as we have seen, included in Corner's (1953) list of arillates. One of those, an "aril" in a sympetalous family (Apocynaceae), discussed especially by Corner (1954), has to be struck off the list. Species of *Tabernaemontana* (*Ervatamia*) have a red pulp around the seed, apparently even around the funicle, which seems strange. In some Indonesian species this pulp covers a group of seeds and is an outgrowth of the pericarp from the placental region. It covers or, in the case of dangling seeds, supplants the funicle.

Corner (1976) called it "splitting hairs" to make here a distinction with arils. He reports for other spp. a funicular aril and thinks that in the former group the funicles have changed into the placental lobules found there.

In many Rubiaceae the same pulpa occurs. The extra-ovular outgrowths are often considered as obturators (*Ixora*, *Coffea*), but also as persisting strophioles (*Diodia* spp.) or they form aril-like covers around seeds (*Borreria* and *Randia* spp.). In many Gardeniae the pulpa arises, not from late endocarpal outgrowth but from placental folds already surrounding the young ovules. The whole forms a gelatinous mass around the seeds, sought after by monkeys and birds. We have already mentioned on p. 25 the large fruits (orange-sized) of *Genipa*, known as marmalade box. The pseudo-aril of *Clerodendrum* spp. (red and nicely ornithochorous in *C. Thomsonae*) has already been mentioned on p. 59. Internally folded, glandular tissue in the septa makes the placental parts split apart. It seems a continuation of the pollen-conducting tissue in the style. Also very derived is the pseudo-aril of some Burseraceae in South Africa (*Commiphora* spp.). The putamen of the dehiscent, dry "drupe" after its liberation remains partly surrounded by a red fleshy part of the pericarp (van der Walt, 1973).

The soft sarcotesta mass around cocoa seeds (*Theobroma*) (cf. p. 136) has also often been termed a pulpa. In the banana, the edible mass is a real pulpa penetrating between the seeds with remnants of an aril from trichomes on the funicle. The three filled-up loculi separate easily. The fruit is descriptively considered as just a berry. In reality, it is a hesperidium as in *Citrus*. Of the ancestral aril a vestige remains (funicular hairs).

The endocarp and its pulpa are important features in Leguminosae and Clusiaceae, and probably also in Loganiaceae, but they are best known in Rutaceae and the related Simarubaceae, where an outgrowth of hairs may originally have served as obturator (cf. *Glycosmis*). In *Citrus* and *Aegle* the endocarp forms the edible mass. Sometimes (*Fagara*) it forms a layer around the seeds acting as an aril which attracts birds (Kuhlmann and Kühn, 1947). The



“aril” of the *Xanthoxylum* species, mentioned by Corner (1953, 1964, 1976) seems to be the outer, starchy layer of the testa, easily damaged because it is spongy. *Coleonema* (see p. 142) would point in this direction, but in the literature the juicy mass attached to seeds of *Xanthoxylum* has been described as a part of the placenta.

It has long been known that the clusiaceous and rutaceous endocarp can be split off tangentially as a varied organ in itself, leading to exposure and even autochorous propulsion of the seed (see p.83).

The “aril” around *Actinidium* seeds is a placental pulpa.

The pulpa in Leguminosae will be described separately (Chapter IX, p. 154).

In other, higher, families the endocarp-pulpa acquired (convergently?) the function of the old aril so completely that it separates from the pericarp, except near the placenta, e.g. in *Momordica* (Cucurbitaceae), where it forms the orange bags around the ornithochorous seeds. In *Physedra* such entire loosened “placentas” hang outside the fruits. In Corner’s sense one might consider this as another case of transference (but of what in the family?), as a placental aril. In other gourds, a dry endocarp layer clings to the seed.

Pulpy placentas filling up the space in dry pericarps, though morphologically farther derived, play a comparable role (Melastomataceae). This also necessitates a new term. This case can also be expected (cf. p.57) in Hydrophyllaceae with their exuberant placentas.

## 6. The Pericarp Fruit

**Shift of Function.** The last phase in the evolution of dissemination organs is that seeds have lost all independent power of attraction and that this function (when maintained at all) has become entrusted to the pericarp, together with that of early protection. It will be shown below that this phase was sometimes reached directly in early Angiosperms, bypassing the stage where the seed had the power to attract. Hildebrand (1873) already presented our sequence of means of attraction.

The process should not be seen simply as an orthogenetic outward shift. The new outer layer, the carpel, was plastic and could develop the necessary, secondary mechanisms that were denied to the seed. Its differentiation also means a further separation of the functions of early protection, attraction and late protection (with dormancy), which were no longer situated in the seed alone. The endocarp could take over the function of late protection.

It seems overstrained to consider the process in the light of co-evolution with higher fruit-eaters. These also consume sarcotesta seeds.

“Transference of function” (cf. Corner, 1958, Stebbins, 1970) is a nice term to describe these processes, so long as it is not misused as a causal explanation, and so long as one does not suggest autonomous functions making wild jumps across gaps. This warning remains valid when one describes the transference as “genetic transference”, a shift of gene activity to a different tissue. Perhaps morphogenetic research will reveal that the new layer evokes and displaces the activity of old

genes for sarcotesta differentiation. We have seen that the palisade layer of seeds can also originate from non-homologous layers. The well-known zoological rules for homology and such transference are perhaps less valid for organisms with less fixated differentiation and with open regions for renewal.

Calli of haploid vegetative tomato tissue (in vitro) can autonomously develop pseudofruits with carotene. Substances (bioregulators) have been found that can depress specific genes.

The pericarp fruit is mostly regarded as the normal fruit according to "temperate" concepts (I accept the risk that the first part of this chapter will now be considered intemperate). In fact, the ovary products in this first part might be called "pre-fructus", with seeds still dominating functionally.

In studies of plant evolution the fruit is mostly neglected. This seems partly due to neglect of the previously described tropical and basic conditions and partly to inherent causes, as will be seen (p. 148). Takhtajan (1959) devotes a separate chapter to it, later extended in the Russian edition of the first part of his book. He includes, as the first, some primitive fruits.

Often the pericarp desiccates and then dehisces by means of special structures, which are the main signs of progression here, together with late asymmetry and further postfloral differentiations.

It is now really an organ on its own! When the pericarp remains fleshy and alive, this may be either ecologically functional or not, a difference neglected in most phylogenetic considerations and fruit systems, which merely distinguish between fleshy and dry. When the growing, living "carpels" simply remain succulent, without special differentiation and food-accumulation, the result may be defined as primary fleshiness, a simple lack of prematuration change (as postulated in van der Pijl, 1955 a). Such fleshiness is found in primitive capsules and follicles (cf. p. 136), e.g. in *Sterculia*, *Euonymus*, *Paeonia*, *Macaranga*, and also in *Archidendron*, *Inga*, *Theobroma* and *Myristicaceae*. At this point I must come to Corner's rescue against one part of the criticism of Parkin (1953) and the parallel objection of Takhtajan (1959). Their objection to the senselessness of succulence and the power to attract of supposedly early fruit valves remains beside the point and shows a false understanding of ecology. A valve that remains fleshy and coloured may act as a visual signal. Sclerotisation and dehiscence at special sites are relative progressions from the first condition. A slight physiological alteration in the time of desiccation and lignification may cause such changes, and *vice versa*.

In many cases, however, the pericarp becomes attractive and palatable as a whole, providing zoochory on a new basis and taking over the attractive function of the seed entirely.

We have already discussed for many Gramineae, Labiatae and Leguminosae, and shall later discuss for *Trifolium* and in the chapter on grasses the fact that the covering glumes or calyx can in their turn take over the dispersal function. Many other accessory organs, e.g. the still more outward involucre (as already demonstrated for burrs), the axis (*Ficus*) or the entire plant (rollers) can assist. We shall not elaborate on such further envelopments here.

In some groups the transition to an edible pericarp may have happened quickly in ancient times. *Sassafras* (Lauraceae) already possessed drupelets in the Lower Jura epoch. Some Magnoliaceae, even *Drimys*, and many Annonaceae have already progressed to berries.

**Autonomous Cycles.** One could go on beyond the phase of the pericarp fruit, to spurious fruits or collective fruits with aggregation and further envelopment. If one had a tendency to philosophy, one could follow French botanists such as Gausson or Mangelot (1952) and see the progressive envelopment as a more or less autonomous orthogeny, a cyclic development through the ages, each cycle with a phase of evolution, “surévolution” or involution. This tendency is admitted to be assisted by such factors as economy (reduction of seed size) and selection in the floral phase. I agree that cupulate sorus, ginkgo seed, cherry, apple and fig seem repetitions of the simple sporangium, but this is not simply because subsequent architectural processes have to follow the same course of evolution.

Whereas Mangelot hardly discusses function, I prefer to consider the cyclic, sinusoidal line of dispersal organs functionally – as produced by opposite selection pressures, alternating in importance at different times, as we have described. This alternation must in the main have been between sexuality and dispersal, but at a lower level it must have been affected by changes in circumstances for pollination or dispersal, producing alternation between telechory and atelechory, dehiscence and non-dehiscence and many small seeds versus one large seed; it must also have been influenced by changes in the ovary. All this change means that every time there is again a breakdown of the old way and escape into a new direction, often back to the last but one. The repetition of old organization schemes seems to me a repetition of answers to comparable environmental factors after foregoing change of the structures to suit some other influence. Such repetition is not contradictory to Dollo’s Law as it concerns different morphological elements. This will be demonstrated in detail for Leguminosae in the next chapter.

Mangelot teaches us that development of a new enveloping organ causes compression of the earlier organ and that the type of Monimiaceae (as described on p. 134) or *Ficus* represents the contracted flower of the future.

In my opinion, the retardation and reduction in size of orchid ovules were related not only to the compression by overdevelopment of the flower, as stated by Mangelot, but mainly to mycotrophy and old anemochory in the ancestry (cf. *Apostasia*, where the seeds are already reduced, though the flower is still simple).

Parallelisms and repetitions in flowers have also been indicated as autonomous. There too, ecological insight has been able to refute such concepts (van der Pijl, 1958).

**Further Evolutionary Influences and Processes.** At this point, having arrived at the “normal” fruit of modern times, some remarks on further evolution may be useful.

I shall not take up a stance for all incidental references to fruit evolution in angiospermous groups.

The first difficulty is that the higher development of the flower as a more centralized pollination organ has also influenced the ovary and thus the subsequent structure of the fruit, as has already been substantiated on p.17.

For other reasons I doubt the possibility of finding general evolutionary trends in the life of the pericarp fruit itself – even if one agrees with the much-doubted monophyly in the origin of angiospermous ovaries and fruits. There seems to exist specialization in all directions, with regression and progression and endless convergence.

Egler (1943) gives a system of his own and mentions fourteen points of evolutionary progress in the fruit, meaning the common pericarp fruit only. Most of these, however, refer primarily to the flower. These can serve for mere description and typological classification, but not for marking general evolution in the fruit.

Egler's points 7 and 8 (many ovules or seeds against few) are mentioned as reversible, and thus are less important to us. Indeed, one-seededness can, as argued before, be just a pre-angiospermous remnant or a typical fruit character, but then it may be either primitive (*Calycanthus*) or advanced. It can be connected functionally with the mode of dispersal, and also with simple lack of dehiscence. It may also be just a flower character, a consequence of anemophily in the flower.

Some other points, low versus high, from Egler's list refer to higher functions of the fruit itself – a kaleidoscopic array. One might add (see Stopp, 1950): symmetry of fruit unchanged from the original flower symmetry *versus* symmetry changed on its own. Also, homo- *versus* heterocarpy (amphicarpy) and combination of tachysporous and bradysporous parts.

The intricate, spurious fruit of the old genus *Ficus*, placed high in his classification, is certainly not an end product in the evolution of fruits. It is just a swollen inflorescence, as such indeed specialized, but pollinated by primitive wasps since primeval times. It offers a closed breeding substratum to them. The combination of pollination and oviposition by one insect gave the stability mentioned on p. 134. The persistence and increase of fleshiness of the inflorescence wall after fertilization of its female flowers, and the changing into a "fruit" even before male anthesis, provided a very simple regulation permitting endozoochorous dispersal after the preceding monovuly or monospermy.

My evaluation of these points as "progression" in the pericarp fruit may be clear from the foregoing. They should not be applied to fruits in general, but only to restricted groups where the floral aspect is of equal order. One should be extremely prudent as long as the possibility of acarpellate seeds and ovaries and the polyphyletic, convergent origin of carpellate structures has not been withdrawn from circulation.

Stebbins (1970) accepts for a parallel study of evolution most of our developmental phases, save the (apparently mistrusted) basis of the sarcotesta and the humid tropics. He elaborates on the changes in some groups, placing for



the background the emphasis on a change from moist to xeric mountainous zones, zones considered as original for Angiosperms. Soft seeds with weak dormancy do not fit into this concept, where protection is of overriding importance and wherein recognized ancient connections of flowers with beetles and of diaspores with reptiles seem less relevant. Are all soft seeds and is all megathermy derived? See also p. 131, 161.

We shall test our concepts on two families.

## IX. Ecological Developments in Leguminous Fruits

This review has a mixed character. It shows, first, the late plasticity of the fruit during speciation, acting also via dispersal. It is also to some extent a typological classification of the fruits, to some extent a trial in the direction of organ phylogeny, in both respects with emphasis on the ecological background. We shall not enter into the eternal general question of whether form or function is primary, but have here to emphasize the bonds with the biotic and abiotic environment. The flavour of circular reasoning may be excused. Selective forces and structures with their feedback systems do have a circular relation. The review (which has previously appeared in van der Pijl, 1956) must also try to maintain contact with current taxonomy, perhaps assist it. The result will show that, although the Mimosoideae again prove basic, it is possible to align the developments in the three subfamilies, where the limits are sometimes vague.

Some words on the leguminous seed: following up the work of Boelcke (1940), Corner (1951) uses special criteria to link and separate the old subgroups anew. In his anatomical derivation, he somewhat neglects the functional differences and also the influence of non-dehiscence of the fruit, which may induce regressive reduction of the seed coat, not to be confused with primitivity. In his fear of premature ecological conclusions, he ascribes to the pulpa only the role of maintaining the turgidity of the embryo. I just mention his general conclusion to the effect that the papilionoid seed is a specialization of the mimosoid-caesalpinoid seed. In Corner (1976) more details are presented.

The Leguminosae are well suited to an inquiry into the ecology behind seeds and fruits, isolated from other processes, because the flowers are always entomophilous (except in *Hardwickia*) and because their ovaries are simple and uniform. The Cruciferae are equally interesting for a dispersal spectrum of a family, but are a late, herbaceous group also more complicated in possessing more derived ovaries (Voytenko, 1968; Zohary, 1948). Here fruits can even be the basis of classification.

One-seededness can be found with many backgrounds. As I said before, I reject the background of an orthogenetic trend to singleness, and also refuse to invoke "advancing sterility".

Following the general lines in Chapter VIII, we shall see that initially the seed still dominates functionally in dispersal. The fruit in this first phase is a follicle, a container for seeds which themselves possess auxiliary organs. Later on, fruits evolved, which are descriptively listed as: drupe, samara, moniliform pod, lomentum, craspedium (a lomentum with persisting sutures forming a replum), achenium, utricle, legumen. Some queer, mostly unnamed forms are:

dry fruits with separating dry endocarp, fruits with a fleshy endocarp-pulpa, and a drupaceous lomentum with the hard endocarp jointed (crypto-lomentum).

These forms have developed convergently in many tribes, where ecological specializations reign in a parallel way. Such groups are taxonomically considered as units (also as genera) for other reasons, mostly because of floral structure. Bentham, therefore, concluded in 1875 in his monograph of the Mimosaceae that fruit forms should not be used to split genera here. Instances of genera with very polymorphous fruits are *Acacia*, *Pithecellobium*, *Cassia* and *Erythrina*. Some authors, nevertheless, split genera with fruits as a criterion. The fruit genera, apparently, do not yet overlap with floral genera.

We also met strong ecological variation in seeds (see e.g. p. 133) and saw the capers of Corner's arils. It is, therefore remarkable that he (1976) concluded on p. 165 that seed structures will become the basis for the natural classification of the Leguminosae.

We cannot sketch the differentiation within each floral genus separately, and can only occasionally trace the evolutionary trend therein, even though some genera (e.g. *Trifolium*) fully deserve such treatment. Incidental remarks on various genera occur throughout the book and may be located by consulting the index.

The methods of dispersal in African Leguminosae have been described by Buchwald (1895). His paper contains some wrong assumptions based on herbarium botany only: they have been criticized by Ridley (pp. 205, 206, 346).

Lhotska and Chrtkova (1978) did so for Czechoslovakia.

Connaraceae, possibly somewhat ancestral to Leguminosae, possess seeds with a sarcotesta and derived products and are basically ornithochorous, too (Leenhouts, 1958).

We start with some primitive and still arborescent Mimosoideae, first the large genus *Inga* in South America. The data accessible to me are scarce and scattered, but it seems that we are here still at the simple level of beginning general zoochory with divergence according to dispersal by fish, reptiles, birds and mammals. The seeds are uniformly surrounded by a white sweet pulp (also popular with man) which is sometimes adhering to, sometimes easily detached from the nude embryo. I have never seen an exact ontogenetic investigation, but most authors consider it a sarcotesta, a transformation of the integument, although sometimes it adheres to the endocarp and integrates its juicy outgrowth with one from the pulpa.

The sarcotesta seed is not well exposed. The whole fruit drops at maturity and does not dehisce regularly. According to Huber (1910) and Kuhlmann and Kühn (1947), fish like the pods, and these are often found drifting. Perhaps a.o. *I. aestuariorum* is in this way bound to river banks. The fact that the nude embryo is easily released points to some bond with water, as also testified by the frequent vivipary (cf. p. 119 and the situation in *Eperua*, discussed on p. 24). When maintaining the theory that Angiosperms originated in (xeric) mountain regions, one has to compromise by agreeing that non-dormant sarcotesta seeds were just conserved in rain forests.

The simple pod of *Inga* can hardly be considered as specialized.

Kuhlmann found intact embryos of *I. sellowiana* in monkey excrements. The embryos thus seem to possess (? chemical) protection against crushing. In some species, the fruit dehisces more or less, or can be opened, and, though it is not reported to be coloured, their seed is popular with birds. For *I. feuillei*, see Borzi (1903). Here the outside of the embryo is cutinized.

The anatomy of the pericarp has to my knowledge not been reported anywhere, and the presence of endocarp fibres as a dehiscence mechanism should be investigated especially. Perhaps *I. ciliata* forms a transition to an arilloid.

The related Australian form *Archidendron*, florally advanced, though primitive by its apopolycarpelly, shows some torsion of the valves, although often the process just provides side-slits. The red fruit with sweet sarcotesta seeds is typically ornithochorous, like the fruits of the *Sterculia* and *Paeonia* species mentioned on p. 136 (see Fig. 3). According to Fahn and Zohary (1955), the anatomy of the valve layers is also of the simplest type. In this case, it seems primitivity, not regression due to secondary indehiscence, which they did not distinguish in their (descriptive) paper.

In regard to Corner's (1976) denial of the presence of a sarcotesta I remark here that this reposes only on one herbarium-study, where it was not observed. Other authors saw it on live material and I refer to the parallel case of *Ormosia* (p. 154). Stebbins (1974) considered the fruit as specialized because of the characters just mentioned. He neglected the seeds.

The pantropical genus *Pithecellobium*, related to *Inga*, is here considered *sensu lato*, neglecting the splitting into fruit genera. Its evolution seems to start with ornithochory of sarcotesta seeds, permanently exposed and sometimes dangling on dehiscing or partly dehiscing valves, which are often coloured. Instances are *P. ellipticum* and *P. microcarpon* (with a red fruit). The torsion of the valves, caused by fibre layers in the endocarp, seems functional as a presentation of berry seeds, as is the case in other ornithochorous fruits.

In many species (such as *P. dulce*, *P. diversifolium*), the dehiscent pod presents arilloid seeds or (in *P. clypeatum* and *P. lusorium*) mimetic, blue seeds. When describing the seeds as exarillate, it is necessary to distinguish pre-arillate from post-arillate conditions.

Almost all other types of fruit mentioned in the beginning of this chapter have (? consequently) evolved in the genus, which apparently never produced a common legume for use outside forests. Pods dropped for ground-ruminants are frequent in *Samanea*. Arilloids have been abolished in these pods.

That Leguminosae originally had the attractive part outside the contents of the seed proper (to be protected against crushing and predation) seems connected with the multitude of toxic compounds inside their embryos. This may also be connected with the nitrogenous nature of its reserves. It stands in contrast to the atoxic nature of cereals (see p. 165).

In the genus *Acacia*, sarcotesta and arilloid have in many species been replaced for ornithochory by the curious swollen funicles mentioned on pp. 37



and 139. Orange funicles around black seeds point to the ornithochory mentioned there. Janzen (1969a) reports that whole rows of seeds united into one pulpos mass hang from the pods of *A. collinsii* and *A. hindsii* and are eaten by birds in Central America. The nature of the pulp should be investigated. In other species, mainly African, the pod became pulpy and indehiscent. Arilloids are superfluous there. *Albizzia* has a different aspect, with more anemochory and hydrochory and without arilloids.

The Piptadenieae represent a compromise, being high trees with pod-follicles that dehisce in one or two sutures, liberating without explosion winged, anemochorous seeds. These are exceptional in the family (and pointless in herbs). The wings of African species may be derived from a sarcotesta, of which the American representative *P. excelsa* still shows a trace.

In the subfamily of the Caesalpinioidae, arilloids are very frequent (*Afzelia*, *Copaifera*, *Sindora*, *Swartzia*, p.p.). They mostly serve for ornithochory, and in *Swartzia prouacensis* dispersal is by bats (cf. p.52). In Amazonia for fluviatile *S. polyphylla* turtles join in. The African genus *Schotia* even has some species with a primitive parenchymatous testa, not induced secondarily by occlusion. Many species have arilloids, but a craspedium (replum) also occurs (Pitot, 1960). *Cassia* has abandoned the use of arilloids and specializes (like *Hymenaea*) in pulpa fruits for mammals, but also has lomenta, legumes and even a winged, ballistic "Rinnenhülse" in *C. alata*.

The Papilionideae show a different seed development, aimed more in the direction of dormancy and help from the pericarp. They tend to variation in the pod itself, the range often being extended to form a legume. This is not the basic type, although it is fixed in the European mind as such. Its autochory is a sign of a pioneer character, prevalent in herbs and shrubs. Its twisting endocarp is just a newly utilized remnant of the *Archidendron* condition. Sometimes vestigial arilloid structures are left; these are usually referred to as strophioles. They may be remnants of an arilloid or just a funicle top as in *Acacia*. In some forms (*Stizolobium*) it is still large.

We are now gradually leaving the genial, humid environment, as leguminous trees had to do in many regions after geological and climatological changes.

Some Leguminosae had to find a compromise between attractiveness of seeds and strong dormancy. A way out was the deceit discussed as mimesis on pp.40–44, which maintained ornithochory of the seed although the latter grew very hard and dormant.

As we said there, the imitative type arose on a sarcotesta – or arilloid – basis, not entirely *de novo*. The occurrence of this type in all three subfamilies points to a model of old stock, to ecological parasitism on preexisting berry-seeds. Even the Papilionideae found this way, perhaps especially, as exemplified by the best-known case: that of *Abrus precatorius*, the single representative of its genus. The genus *Ormosia* has predominantly "coral seeds" (*hormos*=necklace). The

derivation is simple when we consider *Arillaria*, indicated by Corner (1951) as a priceless relic from Burma for his "Durian Theory", but taken over here as such to parade as our saint. It is in all other points an *Ormosia*, but has a juicy layer around the seed, called aril by Corner, although it is probably a sarcotesta as in *Archidendron*. (In the latter genus, too, taxonomists call it an aril.) Merrill and Chen (1943) have proved this, finding a sarcotesta in other Asiatic *Ormosia* spp. as well. They deny the possibility of considering the red spot or coat to be a concrescent aril. Corner (1976) ignores this paper.

In *Erythrina*, mimesis developed in many species all over the world. I could not trace concurrence with taxonomic sections or variance in habitat. The genus has further developed all possible kinds of fruit for many modes of abiotic dispersal, neglecting the mammals. *E. lithosperma* has hemilegumes, each half forming an anemochorous samara. More primitive species have simple disintegrating pods sometimes with seadispersed seeds.

In some basic Sophorae (*Baphia*, *Leucomphalos*, *Bowringia*) permanently attached coral seeds, red or bicoloured, are found with strophiolae. Are such strophiolae elaiosomes?

Here the principal role of seeds ends. The fruit-wall takes over completely. We have already encountered this phenomenon in pulpate zoochorous fruits in savannah regions, which are swallowed by ruminants, monkeys, etc. (see p.48). A transition may be assumed when the pulpa clings separately to the seeds, which are picked individually by birds. Osmaston (1965) and others observed this in *Parkia filicoidea* (Mimosoideae).

The pulpa is present in the three subfamilies, in some species of *Cassia*, *Dialium* and *Gleditschia*. It probably is already in existence in some species of *Inga*, such as *I. jinicuil* and *I. densiflora*.

In *Swartzia* and *Pithecellobium*, the pulpa alternates with ariloids. Traces of endocarp proliferation are still visible in *Vicia* and *Phaseolus*. The endocarp separates from the rest as an anemochorous wing in *Schizolobium*.

The pericarp as a whole can in diverse groups become semifleshy and the fruit indehiscent for use by ruminants, etc. (*Tamarindus*, *Ceratonia*). This has happened to a large degree in African *Acacia* species. In diverse tribes of the Papilionoideae and Caesalpinioideae, the pericarp can even change into a real, juicy drupe, edible for man (*Gourliea*, *Detarium*). In Javanese mountain forests *Euchresta horsfieldii* has returned to the phase of sarcotesta seeds with the pods changed into blue, one-seeded berries.

Many such plumlike pods have in nature been seen to be dispersed by bats (*Dipteryx odorata*, *Andira inermis*, *Cynometra cauliflora*, *Inocarpus edulis*). For *Holocalyx glaziovii* and *Cordyla africana*, this type of dispersal is very probable, seeing that the pod can even produce the typical fermentation odour attractive to bats. The few caulicarpous Leguminosae also possess this type of pod in almost all cases.

The one-seeded fruit has returned to the situation existing in *Cycas* seeds, as in a cycle of Mangenot (1952).

Trample-burrs have already been mentioned on pp.79 and 82, also those Caesalpinioideae with resin pockets in the pods. Langenheim (in Meggers et al. 1973) discussed the (? accessory) possibility of early transoceanic dispersal of such floating pods of *Trachylobium* and *Hymenaea* now in Africa and America respectively. Fruits of *Hymenaea courbaril* are found in oceanic drift.

Development of an explosive pod was easy, utilizing the torsion in exposing valves. This situation is found most frequently in herbs as an autochorous way out, but occurs also in high forest trees, from which large seeds lacking dispersal devices are thrown many meters away. The genera *Castanospermum*, *Pentaclethra* and *Brachystegia* represent the three subfamilies. In some pods the innate torsion, when combined with non-dehiscence, leads to specialized fruits. In *Medicago* this provides epizoochorous balls, in some *Prosopis* spp. the curious endozoochorous screw pods rightly indicated by Goebel et al. as afunctional on this point.

The lomentum, breaking into indehiscent joints, occurs in various groups. The effect is mostly hydrochory and (in adhesive joints) epizoochory (see *Mimosa* on p.97).

Reduction of seed number and of the testa is a natural consequence of indehiscence and transport of the whole.

Non-dehiscence of dry pods, combined with one-seededness, can lead to wind dispersal of circular samaras (*Derris* and *Dalbergia* spp.) or ordinary samaras (*Myroxylon* and the *Tipuana* so often planted along southern streets). In trees or lianas, a slight change can make these relatives, in those genera that live on shores, become river- or sea-dispersed, as is also the case in *Pongamia* and *Cynometra ramiflora*.

The Papilionideae are, from the floral viewpoint, the most derived forms, requiring a very precise bee pollination. The seeds and fruits are often also derived, mostly by simplification. The Papilionideae in the above-mentioned groups with drupes, samaras and water-dispersed pods (in *Dalbergia* and *Sophorae*) show indehiscence and monospermy as part of their respective dispersal syndromes. It would be going too far to investigate which was the primary factor in the deviation from the dehiscing, polyspermous pod.

The more temperate tribes stick to autochory by exploding legumes, for use in pioneering herbs in cold or dry regions. For incidental adaptations in deviating circumstances, and for epizoochory, they provide further modifications and also accessory organs such as swollen or toothed calyces. Some fruits then change into lomenta, some into ballistic organs, burrs or small, one-seeded achenes (see *Trifolium* below). Obviously, this is not an autonomous cycle. In very arid regions the fruits show the reductions in dispersal described before. The giant genus *Astragalus* (1600 species) has already been mentioned under various headings. Zohary (1939) analyzed 100 oriental species, including ballists, rollers, one-seeded calyx fruits and the typical hemilegumes, where the septum provides two halves as independent diaspores.

Table 5. Review of leguminous pods

Morphological classes	Ecological classes						
	Birds	Bats	Ground mammals	Autochory	Wind	Water	Exozoochory
Seed dry, attractive, Pericarp $\pm$ dehiscent $\pm$ fleshy	a) <i>Sarcotesta</i>	<i>Archidendron</i> ? <i>Inga</i>	<i>Inga</i> p.p.				
	b) Mimetic	<i>Pithecellobium</i>					
	c) seed	<i>Inga</i> <i>Abrus</i> <i>Adenanthera</i> <i>Pithecellobium</i> , <i>Azalia</i>					
Seed dry, Pericarp indehiscent, fleshy	d) Mesocarp dry, endocarp pulpa	<i>Parkia</i> spp.	<i>Gleditschia</i> <i>Swartzia</i> <i>Cassia</i> p.p.				
	e) Drupe	<i>Ceratonia</i>	<i>Ceratonia</i> <i>Cordyla</i> <i>Cynometra</i> <i>Tamarindus</i> <i>Prosopis</i> <i>Acacia</i> spp.				
Seed dry, Pericarp dry	f) Pericarp dehiscent, not explosive		<i>Cassia alata</i> <i>Astragalus</i> spp.	<i>Erythrina</i> spp.	<i>Erythrina indica</i> <i>Caesalpinia bonducella</i>		<i>Clitoria laurifolia</i>
	g) Pericarp dehiscent, $\pm$ explosive		Legumen, many non-tropical spp.				
	h) Pericarp indehiscent, large					<i>Vigna, marina</i> <i>Pongamia</i>	
	i) Pericarp indehiscent, seedlike		<i>Medicago</i> p.p. <i>Melilotus</i> <i>Trifolium</i> p.p.	<i>Dalbergia</i> p.p. <i>Oxytropis</i> <i>Astragalus</i> p.p. <i>Adesmia</i> p.p.			<i>Medicago</i> p.p. <i>Astragalus</i> spp. <i>Desmodium</i> p.p.
	j) Idem, accessory envelopment						



The same author (1937) mentions briefly the evolutionary development of synaptospermous devices in the group of Papilionideae-Trigonellae in Palestine, a trend culminating in monospermous, indehiscent pods, so-called nucamentation. Such forms can switch to anemochory or to epizoochory (see *Medicago*, *Trifolium*, *Astragalus*, *Adesmia* in the foregoing chapters).

Table 5 represents a short recapitulation of the main groups. It omits the partly hypothetical oldest relations (with reptiles) and the most peripheral ones (with ants). The scheme suffers from the impossibility of using more than two dimensions so that basic forms share loci with derived ones, returned to the same ecological niche. The first vertical column is certainly not to be considered as a linear sequence.

Many one-seeded pods are eaten together with the foliage by horses and cattle and the pods or seeds excreted in the dung, as is known for many species of *Medicago*, *Melilotus* and *Trifolium*. Diverse granivorous birds pick them deliberately as seeds. Other regulative ways of dispersal occur after one-



**Fig. 26.** Postfloral heads of *Trifolium pilulare* (Israel) with some pappus-like calyces opened, showing the single seeds out of the thin, papery pods. (Photo Natan)



**Fig. 27.** Inflorescence and postfloral head of *Trifolium clypeatum* (Israel). Some (detached) fruit calyces isolated to show likeness to pappose fruits of Compositae. (Photo Natan)

seededness, especially after aggregation (for floral purpose) and after specialization in the calyx.

This situation might, in agreement with Mangenot (1952), be seen as the beginning of a new "autonomous cycle", of contraction followed by new envelopment of the one-seed achene by the early specialized and then persisting calyx, with the latter often taking over the dispersal functions, casually helped by a withered corolla (*Trifolium dubium*) or by plumes from aborted flowers (*T. nidificum*). The swollen calyces of *T. fragiferum* form together a balloon. So do the complexes of hairy calyces in *T. pilulare*, that are detached as a whole and contain a reduced number of fruits. Katznelson and Zohary (1970) gave details on this anemochory in an entire section. In the section Geotropae, with lessened dispersibility, one sp. (*Tr. subterraneum*) became a widespread colonizer assisted by special devices (see p.95) and selfing.

The calyces of other *Trifolium* species (e.g. *T. stellatum* and *T. clypeatum*) approach in the pseudofruit the fruit of the Compositae. The basal part of the calyx encloses the pod (often papery) and the part above the constricted throat sticks up and out like a pappus, often feathery in appearance (see Fig. 24, 26, 27). Pod and calyx base might fuse in the future. In conjunction with the presence of involucre bracts in some species and the aggregation into heads, this new

ecologism suggests initiation of "Papiliocompositae" as a family of future taxonomy. The head tends to develop as one compound flower, with the components as sympetalous tubes (In *Petalostemon*, with the flowers more deviating from the papilionaceous type, we find a parallel development of heads and fruits).

We also see again monospermy accompanied by condensation and indeed in some cases the whole infructescence of *Trifolium* functions as one dispersal unit (roller, burr, balloon or geocarp). There even exists some differentiation within the head, for example in *T. globosum* and *T. subterraneum* where the central flowers are abortive and change into bristles (boring or hooking). After having speculated in Chapter IV on a preluding influence of dispersal upon the flower of Compositae (in the calyx teeth) we can now, after the experience with *Trifolium*, strengthen this view. Probably the calyx, in that case too, was initially loose, with a differentiated upper part for dispersal. Later on, the latter maintained this function, whereas the enveloping lower part fused with the fruit. In still later developments it did so, as a prelude, with the ovary. The envelope thus seems not receptacular.

According to this view, inferiority of the ovary may have started with the fruit in Compositae, although floral influences may have assisted (see p.20). The latter influence is apparently absent in the related family of the Dipsacaceae (monospermous), but evident in other Campanulatae, with many ovules. The site of nectar secretion can decide whether or not such anticipating (preluding) inferiority of the ovary is adverse to the function of the flower. This clash between dispersal and pollination was avoided in the early Compositae and Rubiaceae and in the *Vaccinium* mentioned on p.19, where the glandular part of the torus was raised. The clash is as yet avoided in *Trifolium* and also in some Labiatae, though here too the calyx persists and assists in dispersal.

## X. Dispersal and the Evolution of Grasses

This chapter is not merely a recapitulation, but mainly an application serving to discover again a line in evolutionary processes, aided by special data. As a non-taxonomist, I hope not to commit too many sins in proposing thoughts connected with systematics and that Dr. J. F. Veldkamp (Leyden), who sometimes advised me, may forgive them.

Grasses and orchids are opposites: the first have a multitude of units for pollination but one-seeded fruit (diaspores); the latter the opposite. The first is uniform in pollination but pluriform and specialized in dispersal devices; the latter is uniform in dispersal but strongly diversified in matters of pollination. When considering the evolution of grasses, attention should, therefore, be more directed towards dispersal, not just to the structure of flowering spikelets and components, which we have in our turn to leave aside in favour of function. Flowering is an intermediary move to obtain diaspores! Any general consequences of this approach may be evaluated by phylogeneticists. I am conscious of a contradiction to the opinion on fruits as a basis on p. 151.

The basic unit of dispersal is the indehiscent, one-seeded fruit, the caryopsis. For its background, we have to return to our general considerations on pp.17 and 18.

Monospermy may, in general, be considered as a direct dispersal character, connected with dispersal of the fruit as a whole and with its indehiscence. Such a causal connection can be assumed safely when in the floral phase the ovary still has a number of ovules. This assumption is fortified when relatives, that are florally equal but without the deviating way of dispersal of the species in question, are polyspermous.

One-seededness may in other cases be considered as primarily a floral character, monovuly, determined by the pollination method. The monospermous condition in the fruit then seems a residual consequence. Some cases of isolated anemophiles inside entomophilous families fit in here.

When we leave aside typological approaches (starting from an ideal or "complete" spikelet) of "trend to condensation", "advancing singleness" etc., we have to ask which of the two factors may have influenced the fruit condition in Gramineae, or how they could interact. Shall we again meet a clash between sex and dispersal?

The anemophily of the flower is fundamental for the family and apparently for its monovuly, as for reduction of the perianth. On the other hand, the dry fruit is too typical and too uniform to allow neglect of a possible basic bond with dispersal. Its indehiscence plus monospermy fit the syndromes of both



anemochorous and hydrochorous diaspores, as already became clear in those of higher Alismatales and some comparable Leguminosae. The caryops itself, however, possesses no devices for dispersal and it is rarely dispersed as such. Its liberation together with glumes is significant.

We may approach the nature of the glumes from a functional angle. The bracts do not, at the present time, simply take over the protective function for flowerbuds from the perianth. (I pass over protection of fruits against borers and of young fruits against sucking bugs.) They are too much transformed, hardened, and above all, persistent on the fruit. In the floral phase they (and their awns) seem gratuitous. They do not serve (? any more) secondary release of pollen as scales of cones and catkins. They seem even harmful for anemophily, so that lodiculæ became necessary to ensure good exposition of the "sexual" organs.

We are thus compelled to consider glumes as fruit organs, in some points anticipated in the floral phase. This is obvious for their awns, already fully formed in early floral ontogeny and requiring no influence from fertilization and embryogenesis.

The old name "Glumiflorae" seems better replaced by another old one "Glumaceae" or by "Glumicarpae", at least for grasses, not so urgently for Cyperaceae.

In accordance with this term, for both families I shall use "glumes" for chaffy phyllomes in general and indicate, when necessary, the special elements of grasses by their latin denomination.

The lemma cares most clearly for dispersal and further, this element is most important for diversification. The curious special organ, the palea, is also important and is often well vascularized (clearly so in *Oryzeae*). The two usually form a unit distinct in character from the glumae.

The caryops has to rely on these and on other accessory structures of an obviously secondary nature. (The deviation described on p. 116, and below, of *Crypsis*, *Sporobolus* and *Agrostis* spp. are incidental aberrations in derived forms). The accessories have also to be answered for, so that we must ask what agent of transport may have been basic.

As most grasses prefer open places and rely on wind for pollination, thoughts were also directed towards this agent for dispersal. Though primitive-flowered groups live in warm, humid lowland, Stebbins (in Youngner and McKell, 1972) assumed grasses to have started evolution in semi-arid conditions. In earlier work he started a principal line with anemochory as already present, and obviously accepted this as basic (see p.19 on awns). This neglects the circumstance that the caryopsis itself is too heavy and pre-supposes the presence of auxiliary structures as specialized awns, hair-plumes etc., whereas only the glumes (not anemochorous) seem basic. In this vision the influence of theories on semixerix mountain regions as the cradle of angiosperms apparently again plays a role (see p. 149), though it concerns a much later phase.

In classical treatises and books on the family an original vegetative bond with water is often indicated, but dispersal is almost ignored. Some describe types of

diaspores, but actual dispersal mostly remains vague. Agnes Arber, when waiving a general review of dispersal spoke of "a welter of unrelated detail".

Most authors agree that monocotyledons, and especially the groups assumed as possibly ancestral to Gramineae, are more or less aquatic, tropical, perennial geophytes. Therefore, we have to investigate possible old bonds of grass diaspores with water and water animals.

Their parallel development with the recognised aquatics, the Cyperaceae, is striking. The more we stress the differential phylogeny, the more the ecological parallel in the background of the diaspores becomes convincing.

Therefore, we have first to discuss the dispersal of Cyperaceae, where glumes may still serve partly or mainly for protection of exposed floral buds in further less protected hygrophytes.

## A. Comparison with Cyperaceae

A (? still) fleshy pericarp occurs in primitive Cyperaceae. A drupe has also been ascribed to primitive *Scirpodendron* from tropical tidal mud. The mesocarp outside the hard, protective layer is here, however, a dry tissue, serving flotation. Otherwise Cyperaceous fruits are indehiscent achenes, one-seeded and often not really bouyant. As said before, they are often described to possess no dispersal power, but the plants were well dispersed over the world. In the genus *Carex*, in a basically unisexual, terminal subfamily, the fruits are surrounded by persistent, fused bracts, forming a utricle. That this is present in female flowers only, points to anticipation of a dispersal function, perhaps to flotation. Some species, however, had to develop special tissues to assist in better buoyancy. This finally remained un-important or is absent in species where the diaspores do sink in water (Chermeson, 1924). They belong to a type common in waterplants, viz. hydrochorous but also zoochorous in a special way as described on pp. 25 and 33. In early times fish and reptiles may have fed on them and carried some upstream. The diaspores are not ornithochorous in the complete sense, being not coloured and not externally juicy. They are consumed and dispersed by waterbirds (often as their main food) together with grasses (also their fruits) and seagrasses (including *Zostera* fruits). For the greater part they are digested, but the hard cover allows a certain percentage to survive a long stay in the gut of waterbirds, even far-migrating ones (see p. 33). This was long ago observed for *Carex*, *Eleocharis* and *Cyperus* spp. in ducks, especially after heavy meals (sometimes 8000 utricles inside one bird) (see Birger, 1907). Ancient Indians in Nevada caves used *Scirpus* fruits as staple food, but herewith the way to cereals stopped.

Some Cyperaceae bear awns on glumes, but a function (? for anchoring) can be accepted only when they do accompany the diaspores, which is not the rule.

Flotation (not always long-lasting) acts here also or mainly as presentation to waterbirds and other animals. The diaspores (sometimes with glumes) are dropped by means of disarticulation-tissues. In some *Cyperus* spp. axes of

infructescences break into parts in the nodes. In some maritime spp. (including *Remirea*) the fruits on such joints are enclosed by the internodes. We shall find the same conditions in such grasses. In other respects the Cyperaceae provide a retarded mirror of the dispersal in grasses. It still shows an image of the latter's now invisible past (cf. the ichthyochory and saurochory on pp. 23 and 27).

In land forms the emphasis shifted, via ombrohydrochory, towards pure zoochory, sometimes epizoochory (see *Uncinia* p. 109). Secondary developments led to conventional ornithochory in land forms such as *Gahnia*, with lasting presentation on the plant after abscission, as described on p. 44. The inherited abscission had to be compensated for by convergent devices. Other changes are a juicy utricle, colour (sometimes mimicry) or a pseudoaril underneath, often also epizoochory (see p. 33 and 82).

Many forms are xeric and/or montane, but attempts to consider this condition as basic in the family seem far-fetched (see *Scirpodendron*, with which in the tropics early forms in wet forests are related). They (Mapaniae) have drupes, broad leaves and also show a parallel with early forest grasses in reverting to entomophily in the blossoms (here often further derived, condensed pseudanthia).

In contrast to grasses anemochory did not develop in Cyperaceae to a large extent, only in some small genera. In *Eriophorum* accessory hairs make this development possible. They may be derived from the anchoring, barbed and reduced glumes of *Scirpus*, indicated as perigone bristles. These may also provide epizoochory.

In the following parts we shall meet many more parallels between Cyperaceae and Gramineae.

## B. Return to Gramineae (i.c. Oryzeae)

The enveloping glumes of the floral buds must have led to a parallel development in the first grasses, which may be compared with later Oryzeae. It does not seem accidental that the same diplochory as in Cyperaceae (water plus aquatic animals) occurs in many species of this group, to be considered as primarily tropical, perennial and aquatic. I venture to suggest that (at least in dispersal) the Oryzeae are straight successors of the ancestral group in a comparable habitat – permanent open marshes or seasonally inundated grasslands of old flood plains. The ancestral group must have possessed many-fruited spikelets.

Wild *Oryza* spp. are still perennial, and annual species seem here, as elsewhere, secondarily conditioned by either dangerous seasonality, aridity or by cultivation.

Oryzeae have lost the fleshiness and mostly the independence of the pericarp, but they are florally primitive. The spikelets of present forms are, however, considered as specialized, that is as one-seeded. Though *Streptochaeta* is just as specialized, and nevertheless recognised as primitive, this condition led some

taxonomists to place the Oryzeae late in systems. The glumes assist in flotation and submerged hovering, also provide the required partial protection against digestion. Dispersal by water and consumption by ducks are well known for *Leersia*, *Zizania* and *Oryza*. Grazing by mammals on watersides and bogs may help, and fish are also known to devour diaspores. (For Najadaceae this condition has been described before.)

Awns first seem afunctional in an aquatic group, simply relicts of blades, but (considering the water-burrs described on pp. 73 and 81) they may have served for anchoring, as now still observed in *Zizania*. In stagnant water they may act directly as such. When there is some flow they may act in steering the pointed caryopsis into the mud. Later on (see *Vossia* on p. 172) we shall meet a secondary origin of awns de novo under such circumstances and discuss awns as collectors of gas bubbles.

In this respect it is interesting that in *Zizania* only the female spikelets bear awns (this occurs, see Reeder and Reeder, 1966, in declinous higher grasses too). The barbed "perianth"-bristles of *Scirpus* spp. again form a parallel. In the Oryzeae a dry "nut" with a still free seed is present in *Luziola* and *Zizaniopsis*. It was found inside ducks.

The floral position on the top was right for anemophily, but detrimental to dispersal as long as no anemochory developed. Regulation was necessary, just as in the cases treated on p. 24 and 26.

The strong disarticulation of the ripe spikelets (in wild *Oryza* and *Zizania* spp.) now means presentation to the water surface. It has effectively been selected against in cultivated rice, — as happened with spp. of *Setaria* and the disarticulating fruiting axes in maize and wheat.

In other spikelets with many fruits, disarticulation happens in a "callus" either underneath the whole or between the parts. When the spikelet is one-fruited this can occur underneath the glumes or (when lemmas and paleas carry the dispersal-function) above the glumae. In Andropogoneae one male and one fertile spikelet are shed together. Sometimes (rollers and burrs) infructescences are shed. The abscission zone can apparently shift easily, in *Aegilops* over three zones. Sometimes even awns are disarticulated after completed attachment to animals or (perhaps) boring.

Whereas the accessories for dispersal and establishment develop without the influence of fertilization, the abscission tissues may need it, so that disarticulation then fails in unfertilized spikelets. This seems to contrast with general custom, where development of disarticulation-tissue in fruits is prevented by fertilization. Pleading for our concept is the fact that disarticulation without the glumes is practically absent.

The callus is an early preformation, not a relict meristem, not a new ad hoc one (as in leaves), and even not one with plasmatic cells. The general persistence of the abscission, an ancient presentation device, in diverse tribes was described (mainly for France) by Camus (1935). Later Kandeler (1952) elaborated anatomical-morphological details.



In the cases of separate male and female spikelets their glumes and their abscission can also show functional differences. A complete and consistent parallel with Caricoideae (the paleae, comparable to utricles, present in female flowers only) cannot be expected, as unisexuality arose late in grasses and in several lines independently.

In the light of foregoing facts the place of disarticulation (callus) seems less important for classification than is often assumed.

The reduction of pericarp and testa, so basic in the family, also seems to be connected (as in other groups) with the aquatic medium. The grain of rice, highly specialized in this respect, can be consumed without the milling used for other cereals.

The aquatic adaptations in a basic group (and the condition of bambusoids and bamboos to be described next) do not tally so well with an origin in dry mountains, sometimes suggested.

We can point to other indications for an ancient bond with the water surface, before prospecting beyond mere transport in dispersal.

Tropical seeds suffer from attack by seed-boring beetles (Bruchidae etc.). Janzen (1970) demonstrated the vital importance for some *Palmae* and especially for *Leguminosae*. The seeds had to develop toxic substances to withstand these attacks. I pointed before to the general absence of toxic substances in (even large and tropical) seeds of *Gramineae*. This seems an indication of primary non-adaptation to bruchids because of primary life in marshes or pools without such beetles. It is now remarkable that Janzen (1974b) in a study on infested *Acacia* spp. found no such infestation in wet places and later found deviating absence of such toxins in some swamp palms.

We saw on p. 24 that fish (?) and reptiles) seem insensitive to seeds with special amino acids, so that these have no effect.

Cyperaceae and *Zostera* are also poor in toxic substances. We must remark that in *Leguminosae* the edible attractive part for zoochory (if present) lies outside the seed proper, whereas in *Gramineae* the seed itself had to remain edible, though somewhat protected as a compromise.

After further evolution of grasses in dry regions, mankind, harvester ants and weevils in stores could profit from the non-toxicity of caryopses. Weevils (*Calandra*) cannot bore through the glumes of unhulled rice grains.

Another argument to link *Gramineae* and *Cyperaceae*, both in origin are tropical aquatics, might be found in Frey-Wyssling (1935, p. 190, 216). The families both contain (like the *Podostemonaceae* and in contrast to *Arales* and *Liliales*) discrete silica bodies and this was brought into connection with an origin in tropical marshes, with a relative overabundance of dissolved silicates. The occurrence of silicate secretions in other groups does not, however, support this supposition.

The burrowing cotyledonary tube with intercalary growth is considered in monocotyledones to be an adaptation (plumular protection) to a climate or to a biotope with a pronounced dry period or just arid. Should its absence in grasses and the largeness of the already well-developed embryo in *Gramineae* and

Cyperaceae be considered (as they generally are in *Alisma*, *Pontederia* etc.) as indications of a different, more humid, origin? Burrowing under arid circumstances secondarily occurs by devices on the whole mature spikelet. The grass embryo has been characterized as a premature, compressed seedling, not in fear of desiccation. It seems ready for liberation of floating seedlings and for vivipary. For the case of *Spartina* see p. 173. It seems no wonder that cereals can even absorb water from the atmosphere to germinate and that under very humid conditions they show incidental vivipary.

Professor Pohl (Ames) informed me that in (primitive) *Streptochaeta*, culms with still attached spikelets can break over, with the seedlings coming up immediately on the surface. A true coleoptile is lacking here.

In contrast to the first-mentioned burrowing monocotyledones, in grasses penetration of seedlings is directed upwards, to the surface. It is performed (together with plumular protection) by the coleoptile. This organ can adapt its length, until it opens up, to the depth. In *Oryza sativa* this means (excepting special forms) to the level of water above the plant (as experiments proved), even preceding development of roots. Some *Oryzae* germinate only in shallow, water. In forest-forms such as *Bambusa* and bambusoids (especially clear in *Streptochaeta*) a typical, penetrating coleoptile is absent. It seems superfluous on the surface and cataphylls take over protection. In both (as in *Oryzae*) the seedling is more free, connected with the scutellum by a thin mesocotyl. This condition conforms with the haustorial organs of "normal" monocots.

### C. Bambusoid Grasses

We now shift our attention to this group of primitive, tropical lowland grasses that apparently early left marshes and pools for forests, – which are improbable as the primary environment of the family – though Bews supported this. We shall study the apparent consequences of the change to forest habitats. (Some *Oryza* spp. also live in open forests and became awnless – a change easily realized in grasses).

Bambusoid grasses are mostly still perennials and rather hygrophytic, mostly with six stamens, broad leaves and are plants of tropical forests or their margins. Taxonomists include in these some groups, the *Olyreae*, *Parianeae*, *Phareae* and *Streptochaeteae*, sometimes the *Streptogyneae*. Their centre is N. W. Brazil.

The change in habitat affected not only their dispersal but also their pollination, which we shall discuss briefly.

The ancestral anemophily must have been endangered and some indeed switched to entomophily, as already observed for *Olyra* and *Pariana* (with deviating pollen). Sometimes the attractivity for pollen-collecting bees was increased by the increase in stamen number and by coloured, erect anthers. Though it might support the thesis of primitivity, this condition cannot be considered as a continuation of older entomophily.

The groups in question are already unisexual and this makes attraction by means of pollen an imperfect mechanism. Development of extrafloral nectaries,

also near the female flowers, might restore perfect entomophily. They have not been reported for bambusoids, though found in the panicles of other grasses, and perhaps even on the glumae of some *Botriochloa* (*Andropogon*) species.

The shift to entomophily in forests is again paralleled in some Cyperaceae (*Mapania*).

Other bambusoid genera in forest margins could maintain wind pollination by becoming very tall (like bamboos) or by climbing over shrubs.

After having indicated that it should not always be considered in isolation we now return to dispersal.

Anemochory had no chance to develop in a rather dense habitat without strong wind. In humid forests ombrohydrochory could act as a transitional agent. It does so for many weeds in early phases of tropical forests. The zoochory had to find agents but endozoochory, by means of land animals (including granivorous birds), remained weak. The biotope is less inviting to finches and local pigeons are rarely seed-eaters. Water-burrs could change into land-burrs. It is true that these in general are rare in such forests, but they make sense in the undergrowth. Anchoring often develops into exozoochory. Again, this also occurs in Cyperaceae (*Rhynchospora*, *Uncinia*).

Florally most archaic *Streptochaeta* from South America (famous also for its bivalent palea and petal-like lodiculae) have exceedingly long awns on one outer glume of a type that can hardly be considered as primitive. They are thread-like, irregularly crinkled, twining around each other and the bristly top of the protruding main rachis, developed long before anthesis. When the one-seeded spikelets are mature they are loosened, but the coherent mass adjusts this. It exposes the hanging (further prickly glumed) diaspores to passing animals (Reduction of seednumber in a burr is quite common, cf. *Xanthium*). Fritz Müller already observed epizoochory by means of his beard. Often entire complexes are dispersed. (See Fig. 29).

In the African-American forest grass *Streptogyne* we find the same regulation of (here also unwanted) shedding, providing exposition of sharply pointed epizoochorous spikelets, but with a curious transference of function: here persisting long styles (unique in the family) are intertwined and take over (awns are absent). Hygroscopy is absent. We again find a parallel with cyperaceous *Gahnia*.

Below (p. 175) we shall describe parallel cases of compromise between shedding and exposition above ground level in non-bambusoid grasses.

The bamboo-like, mainly American genus *Olyra* has in most species simple, terminal tails on the two glumae. The glumae are dropped at maturity of the diaspores. Before this the awnless diaspores are already conspicuous and exposed. They remain attached, at least for a long time, are very hard and look like the shiny, white diaspores of *Coix*. Ornithochory (perhaps mimetic) may also be assumed in these tall plants.

In the American genus *Pharus* the diaspores are situated between small glumae. In many species they are provided with hooks (absent on male glumes).

The epizoochory has been ascertained. The genus was formerly placed in the *Zizaniae*.

In *Pariana* rachis internodes containing the fruits are shed. They are surrounded by pedicels of male spikelets. This reeks of ombrohydrochory (cf. *Euchlaena*).

Asiatic *Leptaspis* (in the Phareae) is another archaic form, with six stamens. The not-dropped female spikelet (? still) develops a utricle consisting of the closed, inflated, awnless lemma. Hooks on the utricle or on other parts (when infructescences are shed entirely) provide again epizoochory in many spp.

A utricle has also been mentioned for a genus often considered as a dwarfbamboo, *Atractocarpa* (*Puelia*). It lives in Congolese forests. In fact the fruit is an achene with a still free seed, as in many bamboos.

The bambusoid group and its biotope, though archaic, cannot be considered as primary in grasses. Neither is its dispersal system. Awns, when conserved, are clearly not primarily connected with (late) zoochory, but with a new, indirect function for exposition of loosened spikelets. This may be one approach to their exozoochory.

## D. Bamboos

This group also contains perennials in margins of forests. They outgrow the undergrowth and retain anemophily and zoochory and are considered to be derived from herbaceous bambusoid, not polyploid, ancestors (Soderstrom and Calderon, 1974). Awns and the exozoochory, so prominent in smaller bambusoid grasses, seem to have receded in taller bamboos. Regulations against shedding are absent. The distances reached by dispersers are small and the weak colonisation power in general may be connected with the long lifecycle. The fruits are often not (? yet) real caryopses.

In most bamboos the dropped spikelets, without awns and plumes, are dyszoochorous via land-animals (see p.45). As in other cases of apparently "dystrophic" activity by rodents (the main consumers known) the plant has to pay for the transport by heavy losses, just as it does for the transport of its pollen by wind. The gregarious shedding after a longer vegetative life of a larger grass seems perhaps not just an adaptation in the sense of Janzen's "satiation of seed-predators", considering the enormous migration of rats it causes. It (or better the preceding flowering) seems not bound to a climatic cue and not to animal starvation (see Janzen, 1976). The fruits are non-toxic, edible for man too. Even the small, glumed caryopses of *Arundinaria* show no clear anemochory. Some bamboos have a fleshy pericarp, which seems to be, as we shall see, maintenance (and further development) of an old condition, rather than a return from an already fixated, reduced and dry pericarp. Regular connections with fruit-eating birds and mammals, however, are unknown. In extreme cases (see *Melocanna* etc. on p. 119) this condition seems to function mainly as a water reserve for the vigorous seedlings with fast germination (typical in forests) after the dropping,



is connected with lack of dormancy and finally leads to vivipary. Here the food reserve is mainly situated in the much enlarged embryo itself (which already consumed the endosperm, obviating its digestion at germination). In some *Dinochloa* spp. too (see below) the endosperm is used up before maturation. Toxicity of the seedlings (HCN) may be a regulation of the dangers. Such glucosides do develop in young bamboo shoots, also (only after germination) in seedlings of *Sorghum* spp. among others. Troup (1921) considered *Melocanna* to be dispersed by cattle in India.

Some botanists protest against the comparability of Oryzeae and Bambusoideae s.str. They waive aside the primitivity of flowers in the latter because of polyploidy and specialized traits, such as the tree-habit. The latter is, however, not basic in the group. Stebbins (1972) considered them as not primitive, but archaic. Reeder (1962), however, placed both groups in one sub-family (Bambusoideae) for the sake of the comparable embryos, together with Olyreae etc. This combined group of bambusoid grasses has also a comparable leaf anatomy. Since the group contains "dwarf bamboos", it becomes also acceptable that tree bamboos are derived from herbaceous ancestors in shaded biotopes without anemochory. The bamboos, apparently, are an early sideline switched to less aquatic, less open vegetation, when the pericarp had not yet lost the potential for fleshiness and when the seed was still free. The awns lost their function and are absent or nearly so.

Clifford (1961) indicated the possibility of this derivation and the archetypal nature of the flowers of a bamboo for all Gramineae.

In many bamboos the glumes around the fruit become less prominent with the increasing size of the fruit. A dry nut (hard with a loose seed) has of old been ascribed to *Dendrocalamus*. Holtum (1956), trying a new classification of bamboos which was better based on ovary and fruit, describes its fruits as not essentially different from those of *Bambusa* etc. In both genera the top of the fruit has a slightly fleshy apex and remains separate from the seed.

The fleshy pericarp occurs not only in the well known basic group of *Melocanna* and *Ochlandra*, but also in less narrowly related *Melocalamus* and some spp. of *Dinochloa* (otherwise with dry pericarp), thus persisting in three evolutionary lines. This "Schizostachyum-type" is considered as basic.

In more temperate Arundinarieae the "normal" caryopsis, enclosed in glumes, is said by Holtum to represent a progression from bamboos to grasses. (As awns were already lost this is perhaps meant in the sense of convergence to the condition.) Corner (1964) considers juicy bamboo fruits as the antecedents of the caryopsis, but his argument seems less acceptable, when reposing on the vista of grasses as miniaturized palms, published later on.

## E. Open Plains and Higher Grasses

If we accept the foregoing parts, published briefly in a meeting report in the yearbook Dutch Botanical Society 1975, some conclusions about a wider field can follow.

Refinement of dispersal, fixation and establishment must have increased under new conditions, after colonization of varied, open, drier regions, and connected with annuality.

The embryo shows no regression. Reduction of the coleoptile, as shown in *Bambusoidea* (obviously an early side line) is not apparent, though the fixation and burrowing by means of accessory structures now mostly had to precede its ancestral upward growth.

There is no intention of, and probably no sense in considering here diverse tribes separately. They seem to show a parallel radiation in dispersal methods, with reversals in every direction and with, in some groups, a new tendency to anemochory. Some taxonomists found correlation of anemochory and archaism in such groups and considered other ways of dispersal derived therefrom. This does not seem valid for all, nor for the family as a whole, considering the groups discussed before and the rarity of anemochorous glumes.

Though classification in tribes varies strongly according to various taxonomists, Table 6 presents a scheme to compare relationships of cases discussed below. It may illuminate the convergence in methods. That these groups are better colonizers is, of course, also due to their vegetative antecedents, to their general plasticity, resistance to fire and grazing by mammals, of intercalary growth, to their tillering, also to their relatively large, fast-sprouting embryos.

The old accidental endozoochory remains important as most spp. rely on the escape of a part of the seeds from the guts of grazing mammals (so intimately

**Table 6.** Classification of the grass genera discussed in this part of the chapter

Stipeae	<i>Stipa</i>
Phalarideae	<i>Spartina</i> , <i>Cornucopiae</i>
Danthonideae	<i>Danthonia</i>
Cenothocheae (steceae)	<i>Cenothochea</i> , <i>Lophaterum</i>
Aristideae	<i>Aristida</i>
Festuceae	<i>Lamarckia</i> , <i>Cynosurus</i> , <i>Melica</i>
Bromeae	<i>Bromus</i> , <i>Boissiera</i>
Streblochaeteae	<i>Streblochaete</i>
Hordeae	<i>Hordeum</i>
Triticeae	<i>Agropyron</i> , <i>Triticum</i> , <i>Aegilops</i>
Aveneae	<i>Corynephorus</i> , <i>Avena</i> , <i>Arrhenatherum</i>
Agrostideae	<i>Agrostis</i> , <i>Lagurus</i>
Eragrostideae	<i>Eragrostis</i>
Pappophoreae	<i>Enneapogon</i>
Sporoboleae	<i>Crypsis</i> , <i>Sporobolus</i>
Paniceae	<i>Thuarea</i> , <i>Spinifex</i> , <i>Tricholaena</i> , <i>Pennisetum</i> , <i>Setaria</i> , <i>Paspalum</i> , <i>Cenchrus</i> , <i>Panicum</i> , <i>Echinochloa</i> , <i>Digitaria</i> , <i>Lasiacis</i> , <i>Acritochaete</i>
Andropogoneae	<i>Mnesithea</i> , <i>Ophiuris</i> , <i>Rottboelia</i> , <i>Vossia</i> , <i>Miscanthus</i> , <i>Schyzachycium</i> , <i>Heteropogon</i> , <i>Chrysopogon</i> , <i>Botriochloa</i> , <i>Euchlaena</i> , ? <i>Sclerachne</i> , <i>Polyioca</i> , <i>Coix</i>
Maydeae (Zeeae)	

connected with grasses) and of birds (in this case granivorous), (see p.31.46), Ridley gives a profusion of data on seeds (often sprouting) in excreta. Sparrows on the streets knew this before he did. Even the large-grained teosinte, *Zea (Euchlaena) mexicana*, is maintained in Mexican maize fields as a weed by the application of dung from the livestock fed on the removed plants (the break-up of the rhachis, however, points to other natural dispersers). One asks whether the leaf sheaths around the mass of loosened joints here still have some function. The species grows naturally along cliffs and streams and the fruit cases surrounding the caryopses are washed down by sporadic heavy rains. Various *Tripsacum* spp. show this too, according to Dr. de Wet (Urbana). It seems a hygrochastic regulation of shedding.

Some grasses probably reached oceanic islands in or on birds. Ridley mentions this point on p. 561 and discusses (under their respective dispersal classes) many more species than can be treated here.

The burrs and needles involved are discussed below. It is remarkable that (even in desert grasses) myxospory is rare, though on the other hand burrowing makes it superfluous for fixation.

Epizoochory may also repose on adhesive glumes or on small caryopses adhering with soil to feet (p.29) – or even to footwear.

When other functions have been lost or altered on dry, open land, hard glumes still provide general protection during dormancy and transport (especially when endozoochorous), perhaps also against savanna fires. In small



**Fig. 28.** *Vossia cuspidata*, joint with two mature spikelets, the sterile pedicellate one with a stiff tail. The (striped) sessile one has mostly no tail in this species. Rachis internode at right



**Fig. 29.** *Streptochaeta spicata*. Spike with dangling spikelets. (After Ludwig, 1895)

fruits adhering to feet in mud or anemochorous as such, (see p. 181), they are rarely functionally abolished at maturity.

Of course, there exists hydrochory of more derived grasses, secondarily turned to watersides and also eaten by fish and birds, (see p.25). Furthermore, floating power may be fortuitous, not bound to a certain habitat or dispersal method.

Ridley relates that in aquatic *Glyceria* spp. in Europe fruits float for some days simply on the awnless glumes, whereas most other grasses do not. The fruits have been found inside ducks.

More specialized is the genus *Vossia*, well known from the floating sudd on African pools and rivers. Like the other genera in the *Rottboelia*-alliance, it has no lemmar awns, but a hard gluma, often even on the sterile pedicellate upper floret, which produces a broad tip like a stiff tail. This seems a new, incipient awn, apparently repeating the origin of the simple awn of *Oryzeae* (see Fig. 28). Below we shall find much the same for *Cornucopiae*. As in *Rottboelia* (cf. Fig. 14), the main axis of the more riparian *Vossia* spp. described breaks up into loose joints, that float for one or two days. In my bathtub as it slowly emptied, they floated away with their tails at the rear, the blunt bases in front. In nature, however, a whirling current may cause fixation by the tails. After sinking in cool water in the laboratory they rise again with the tails upward. This is due to a very pronounced predilection for escaping, dissolved gas to settle, as large bubbles, on their bristled edges and surfaces, when the water warms up (see Fig. 28). A local naturalist might ascertain whether this also occurs after fluctuations in gas contents underneath the sudd, and then leads to fixation into it. I have to thank Prof. Th. Monod (Paris) for this material and leave a connection with awns in general to experimenters.

One might compare such floating fruit-cases with those (already discussed) of *Euchlaena* and *Pariana* and with those of the aquatic *Rottboelia* spp.



In the mostly awnless, unrelated *Panicum*-alliance some spp. from sudd and inundated fields (including *Echinochloa stagninum* and *E. Crus-galli*) have floating diaspores which bear comparable awn-like, bristled tails on the sterile florets. They too collect gas bubbles and, moreover, move towards obstacles on the curvature of the water surface by means of surface tension.

*Coix lacryma* (growing naturally on river banks and in sudd) makes a hard, floating utricle out of a subtending bract, thus imitating *Carex*. In its tribe (Maydeae) glumes generally do not dominate in diaspore formation; bracts dominate.

Especially higher grasses on sea-shores invented new floating devices with supplementary protection (see *Thuarea*, p.77), sometimes also utricle-like.

In connection with what was said before (p. 166) on the largeness of the grass embryo I point out the marine-aquatic one of *Spartina townsendii*, which surpasses the endosperm in length and volume so that the fruit is a green seedling (embryo) with an appendage. It acquired some type of dormancy, (van Schreven, 1952). Ridley (pp. 254, 331) reports species of this and other sea-shore grasses as being also dispersed by floating rhizomes. Not all such halophytes rely on flotation, but use other agencies. (For *Agropyron* and its polychory see p. 112.)

There also exist secondary forest grasses of xeric descent, convergent to bambusoid grasses with their broad leaves and often having epizoochory of not immediately disarticulated spikelets. In S. Asia examples are *Cenotheca lappacea* and *Lophaterum gracile*. The *Melica* and *Lasiacis* spp. (see below) found another solution. Perhaps the *Streptogyne*, discussed before, belongs here.

In open, arid regions, awns (and other bristles) obtained new functions in higher grasses. There burrs for epizoochory and boring (drilling) devices for establishment became dominant, next to diverse anemochorous devices.

Besides the general, more or less pre-adaptive or "unintentional", endozoochory by birds we rarely find more adaptive, typical syn- or endozoochory. Just as in some *Carex* spp. elaiosomes from diverse accessory parts arose in myrmecochorous grasses (see p.57, 59). In the tropics many more cases can be expected. From Java we know them from diverse tribes, genera *Sclerachne*, *Polytoca*, *Mnesithea*, and *Ophiurus*. Most have disintegrating axes like the *Rottboelia* mentioned, the parts of which species can be transported only by the largest ants.

Cases where non-destructive fruit birds are employed (as occurs in Cyperaceae) had not yet been described, but recently a parallel to forest-dwelling *Carex baccans* (p.45) was described for a forest edge grass genus, *Lasiacis*, (formerly included in *Panicum*) from Central America. Some spp. develop berry-like, black spikelets, ignored by granivorous birds, but dispersed by real fruit birds. This happens without damage to the seed, which is protected by a hard lemma and fertile palea. The glumae and sterile lemma become black and juicy, and store oil at maturity of the caryopsis (Davidse and Morton, 1973). This confirms the old rule (previously pointed out for bamboos), that a new attraction does not return to its former organ, in casu the pericarp. Other *Lasiacis* spp. are mentioned (also woody climbers in edges of forests) as having dark, globose, but

bony-hard mature spikelets. As they are shiny, mines is a possibility. Abscission is only postponed, not regulated by special means as in epizoochores or in *Gahnia*. The data in Ridley (p. 149) on anemochory in North African *L. hirsutus* (untraceable!) may repose on some error, though the genus has a short woolly tuft.

In the "normal" grasses, which colonize in open fields, dispersal by wind had a better chance. Reduction in size of the caryopsis assisted here, with the side effect of excluding internal parasites.

Anemochorous devices, curiously, never consist of persisting styles on the caryopses themselves. They are: rolling complexes, balloon-like glumes, hairs from diverse parts or elongated or plumed awns. We saw, however (pp. 69, 82, 111), that as true colonizers they use much polychory. The sharp bases of many spikelets serve both boring and epizoochory, their awns serve epizoochory (sometimes being sticky in *Hoplismenus*), but also anemochory and atelechory. To use one example: *Lamarckia aurea*, an originally mediterranean weed, detaches complex diaspores from the main rachis. They are the fascicles consisting of one fertile and also two sterile (fleecy) spikelets, that are not abscised and take over, enlarging the surface for the evident anemochory. The fertile spikelet bears long, anchoring, terminal awns (not hygroscopic). The diaspore can also adhere to and prick into clothes by means of its pointed and bristled base, reminding us of drilling diaspores. *Cynosurus* is related and has comparable diaspores, but the sterile spikelets (the "combs") are further reduced and do not assist. Also in other tribes accompanying remnants of male florets may, as division of functional labour, be specialized for dispersal inside a complex diaspore. As discussed below, in some *Bromus* spp. the empty upper lemmas of the complex diaspore may assist in drilling.

In some species of *Holcus* and *Arrhenatherum* (Aveneae) the male one of the two florets which are dropped together at maturity provides the functional awn. This condition only seems to deviate from the rule, mentioned under the Oryzae, that males need and have no awn. This rule concerns male spikelets of florets which are permanently separated from the female ones. It is not valid when the products of both co-operate in the diaspore. This, as said, occurs in many more diclinous grasses. I refer to the aquatic *Vossia* and *Echinochloa* discussed before and to *Lamarckia* for other ways of co-operation between "sexes".

We may remark here, along the lines indicated on p. 18, that in such cases of monoecy the differentiation of "sexes" is also connected with dispersal. Androdioecy in *Spinifex* (p. 69) is clearly connected with reduction of the number of fruits in the giant diaspore of one "sex" and a balancing, large quantity of pollen in the male. Gynodioecy (the reverse) in other genera (*Danthonia*, *Cortadenia*) has been shown to provide more and better-dispersed fruits on separated females. These cases are rare extremes. Very common is dicliny between near-by flowers or spikelets. This is not of the usually accepted, simple "sexual" nature (promotion of cross-pollination). It did not, in grasses, lead to a general dioecy, as one might expect in anemophilous plants. For a general discussion on such matters see van der Pijl (1978).

In desert regions round infructescences often break off and roll away, as a whole. Ridley mentions spp. of *Agrostis*, *Panicum*, *Dimeria*, *Spinifex* and *Eragrostis* – a very heterogenous group. Hygroscopic or other intertwining of awns, repeating the method of *Streptochaeta*, may sometimes serve the development of rolling complexes of fruits only (meteoranemochory), as seen in *Aristida funiculare* and some *Stipa* spp. In other cases, as in deviating S. Asiatic *Heteropogon* (*Andropogon*) *contortus* from arid savannahs, it serves lasting exposition of pricking complex diaspores high on the plant. Here the terminal awns (on the female spikelets only) already intertwine during anthesis but pull the spikelets outwards after abscission. Though kneeless, they may also provide some drilling after landing, using hygroscopic untwisting in the spiralized basal part. The upper part, however, is often sinuous, serving more the intertwining than the usual arresting on the ground. The spikelets proper easily break off from the awn when pulled, so that epizoochory seems to prevail. They have been found in sheep's muscles. In some *Stipa* spp. the intertwined balls also bear the pointed caryopses on the outside (see Ulbrich, Fig. 49). Such (? collateral) exozoochory may also be a background of the awn-abscission found in *Stipa*. *Chrysopogon* (*Andropogon*) *aciculatus* (short awns) regulates inherent shedding for possible epizoochory in a simpler way. The abscission tissue underneath diaspores (containing male spikelets too) is positioned obliquely, as in other "needle grasses". After a contact it loosens them first at the bottom, so that sharp bases are pointing somewhat sideways at the periphery of the infructescence.

*Streblochaete* (*Koordersiochloa*) *javanica* shows the same phenomenon as the *Heteropogon*, though belonging to a different tribe. The dorsal awns are very thin and kneeless. They are so strongly intertwined that complexes have been found on passers-by. In *Acritochaete* spp. (from montane African glades) bunches are formed by intertwining of thread-like, terminal awns from glumae and lemmes. The complexes are easily detached. Does intertwining (already present in *Streptochaeta*) offer a background for spiralization of awns in general? The internal spiralization of an apparently straight columna may then be considered as a division of labour in the awn, allowing the straight part to penetrate during burrowing while the pushing part remains outside.

We already discussed diplochory of *Agropyrum*, *Spinifex* and *Stipa* (pp. 69, 112). Some *Melica* spp. produce both anemochorous and myrmecochorous diaspores in one spikelet (Sernander, 1906)!

We are not yet sure of the ecological significance of the isolated myxospory by mucilage from the pericarp on liberated seeds of *Sporobolus* spp. (drop-seed grass), as indicated on p. 116. It is typical that here the testa is relatively well-developed and that the dehiscent caryopsis is often exposed on top of the culm by the wide spreading of glumes, and further is typical that disarticulation is deferred or replaced. All of this shows the reverse background, viz. lack of shedding, but seems functionally comparable to the devices for exposition in the described *Heteropogon*, *Streptochaeta* and *Streptogyne*. Epizoochory agrees with such species which frequently occur along footpaths. The impression is that in species from deserts the dehiscence of caryopses becomes less dependent on

hygrochasy and that myxospermous anchoring of the dropped seeds, by subsequent wetting on the soil, becomes more prevalent there.

## F. Some More Remarks on Awns and on Establishment

Awns are specialized reproductive organs, formed very early in ontogeny. Many taxonomists loosely describe awns as (eventually loosened) midribs, which are then inserted below the top or at the base of the glume. Others stick to the morphological concept of the awn as the reduced leaf blade on top of a transformed sheath, or situated dorsally beside transformed ligulae.

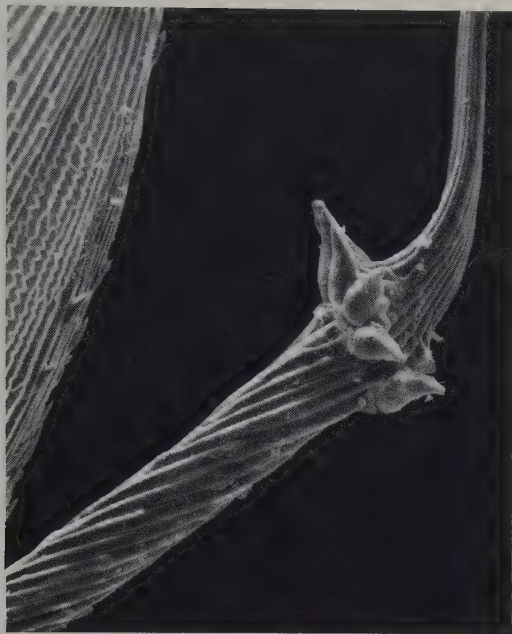
Though we are here interested in convergence in ecological devices and its causes, we have to refrain from delving into the morphology of the lemma and its awn. I refer to a study by Tran Van Nam (1973); she maintains that the typological concept of awns as blades demonstrates the rest of the phyllome as also being present, but with differential development of vagina, stipules and ligula, resulting in morphologically differing lemmas. Even in an awnless lemma a blade and a ligula are here recognised. We have to leave aside the nature of the queerly converted lemmar awn of "hooded" barley.

Rarely subtending foliage leaves take over from the glumes for some functions, when covering complexes of spikelets. In secondarily hydrochorous *Coix* and *Thuarea* they remain protective and sheath-like, also in awnless *Cornucopiae*, where the dropped complexes of spikelets have been indicated as drilling but seem better constructed for flotation. The plant lives in Oriental marshy places near streams. Does this second-order spikelet with second-order "glumes" spread light on the original function of glumes?

In another genus, Mediterranean *Crypsis*, the upper part of the involucre leaves becomes awn-like, hard and sharp. The complexes on the low rosette plants change into trample-burrs, as in *Cenchrus*. Again second-order spikelets repeating the formation of awns? Why the enclosed caryopsis became dehiscent here is another question.

Awns may become long and thin, serving more for anemochory, especially when hairy, but this does not seem to be their primary function. When rachis hairs, or others, care for anemochory an awn may persist for the primary function of fixation (*Miscanthus*, *Lagurus*). Basic anemochory within the family might again be concluded from Stebbins' remarks on dispersal (in Youngner and McKell, 1972), where even anemochory of *Setaria* is assumed. Awns usually continue to function for fixation, now on land, and for establishment; this is probably the crucial phase in competition. On p. 117 this was discussed for a *Danthonia* with a "median" awn between two lobes. We may pass over a function, as alleged in some Russian papers, to be a repellent to grazing animals. Also any physiological significance is not discussed here. Many awns in arid regions undergo torsion, leading to hygroscopic movements with a drilling effect, though in some this serves the liberation and/or the exposition of diaspores. The drilling arose in different groups, obviously as a regulation for the unsuitability





**Fig. 30.** *Corynephorus canescens*. The awn spread side ways during photographing. The "cogwheel" between basal and upper part. Note now deviating surface of lemma facing cogwheel. (S.E.M. photo Brantjes)

under aridity of the coleoptile growth described on p. 166. A role of contractile primary roots to obtain depth is unknown. The necessary sharp basal points arise convergently from oblique abscission of the caryops itself or from adjoining rachis parts (cf. Fig. 24 a).

Amongst the Aveneae I mention *Corynephorus canescens*, a pioneer from dry sands in Europe. The basal awn on the lemma has here a deviating construction, bearing a corona of hard and sharp, radial spikes around the tip of the spiralized, brown part (the columnna), and on top of it a glassy, club-like part (subula). The latter is rough by the tips of the sclereids, a little twisted. It is dorsiventral, bent sideways when dry. The whole awn is 2 mm long and the diaspore proper is 1.4 mm, and has the bristled, sharp base of all drillers (see Fig. 29 and 30).

Linsbauer (1933), when describing the internal anatomy, indicated that the awn makes the dropped diaspores jump after being moistened on a smooth substrate as in other Aveneae (see p. 89). The awn turns at first very quickly in one direction, later suddenly in the opposite one.

The sudden disturbance of equilibrium seems more especially promoted by an initial arresting of the moving parts, not only against the substrate but also against the lemma. This happens, (a) by the sideways swinging (when not yet saturated) subula against the tip of the lemma and (b) by the corona spikes rolling over its surface.

After moistening (and in reverse after drying) the cogwheel rolls with growing tension over the cell walls of the lemma, with vivid shocks. Seen from above the tip of the subula turns clockwise in moist air, then is superseded by the columna turning anticlockwise, which takes a longer time for reaction.

Though already present, the movements have not yet a function at anthesis, but provide later, on a rough substrate, the drilling in of grains. The shocks seem essential to the process, especially the first shock, which acts like a shot. The subula brings the grain immediately, or by its first swing, into an oblique position ( $30^\circ$ ) and, if the point is then arrested on the ground, the shock provides first penetration (or a jump when not arrested).

I could confirm this with a small experiment, by placing grains on a disk cut from fine-meshed, spongy plastic. It was alternatively mist-sprayed and dried by radiation. Jumps were rare here. Many immediately took a  $45^\circ$  position in pits in the mesh and became embedded in a few hours, penetrating the mesh obliquely. With grains orientated vertically in the pits, where the awn could swing freely, no penetration occurred (Linsbauer verified this by cutting off the subula). To test this further, grains were placed on top of a tube filled with sand, which was alternately wetted and dried. After 3 days a considerable number were found embedded to a depth of 2 cm.

The twisting and the shocks of the rolling cogwheel could be followed well in diaspores which were pricked vertically into the plastic disk.

The "curiosity" now proves to be a precision instrument, imitating a concrete drill, more refined than that of *Avena*. The jumping is accidental, as Zohary pointed out long ago, but it can have some significance, not for dispersal but for attaining a spot with better microrelief.

Zohary (1937) already performed experiments with other trypanocarpous grass diaspores (with knees in the awns) proving that the position at landing could be decisive. In this respect he found differences between some *Stipa* spp., and considered among *Avena* spp. *A. sterilis* to be inefficient. Those straight-awned diaspores that can also be moved in only one direction, but do not actively drill in, only enter cracks or fissures passively (by wind), like those of most *Aegilops* and *Hordeum* spp. he called *Keilfrüchte* (wedge fruits). In some *Aegilops* spp. the straight awns spread aside hygroscopically, providing a better angle for entering. Figure 24 should be reconsidered in this light, with a warning not to rely on assumptions based only on structures. Epizoochory is collateral in *Hordeum* spp. and others; so is eolic drift.

A separate point is the possibility that drilling in or wedging in affects the position for germination. Experiments with *Bromus* spp. showed that even on British loam the position of the embryo in microsites on the surface was decisive (e.g. Harper, 1970). A compromise between the concepts of drilling in and creeping away (see p.87) was reached by the experiments of Peart (1979). The creeping may result in reaching a microsite favourable for drilling in. They also confirmed the above concept of Zohary and Harper, that non-motile divaricating awns or bristles provide (see p.87) the right position for water uptake via the scar. I also refer to the conclusion of Simpson (1952) (see p. 117) who also regarded

*Schizachyrium fragile*, where the passive awn co-operates with the twisting one by braking its movements until the tension leads to a forceful jerk.

Many taxonomists adhere to an old typological reasoning (of Duval-Jouve from 1871), that the complete arista consists of a spiralized columna and an upper, straight, part (subula). Awns consisting of only the latter are considered as incomplete (setae). "Complete" awns are ascribed only to lemmas.

In this light the terminal, straight and simple awn on lemmas of Oryzae and other non-boring grasses and those on glumae must be derived and simplified, which is evolutionarily improbable.

This is not to be glossed over by such typological tricks as a "latent presence" of the higher in the lower, in the form of an immaterial "idea" of pure form.

We should also ask whether all spiralized columnas are homologous, e.g. in *Avena* compared to the *Stipa* alliance, where it is ontogenetically a deviating, late development.

In *Stipa*-like grasses the twisted "column" looks like the apex of the lemma, which in some is provided with three setae on top. Is there homology with *Avena* or transference of functions to different organs?

In some *Stipa* species the median awn of the three is larger and is plumed. This secondary device may simply lead to collateral anemochory or may provide a fluttering, which assists in drilling. Sometimes all three are equal or plumed.

The presence of mere functional analogy in the drilling devices, necessary for burrowing the seedling into dry soil, is probable, as the drilling developed independently in different tribes. In the *Aegilops* and *Hordeum* spp. described, complexes on disarticulated rachis parts are involved in passive penetration.

The transformation of awns can occur within one genus without apparent differentiation in habitat, e.g. in Asiatic-Pacific *Garnotia*, where all species concerned are said to love moisture and shade, and often occur on streambanks. We find here a terminal awn, which can be (a) nongeniculate and straight, (b) just geniculate, (c) geniculate with a twisted columna or (d) straight with a thin, long and crinkled upper part. Awnlessness also occurs, and in different subgenera.

The dense infructescences of *Lagurus ovata* (also from arid Mediterranean regions) look like woolly eggs with their plumed, awn-like, glumae. The long, boring awns (geniculate with a twisted column) protrude from the lemmas. They already perform hygroscopic movements in situ. The whole infructescence and the glumae seem afunctional for simple anemochory. The latter are not finally abscised, as the rest of the spikelets are. The agent for the detachment of these diaspores is not clear. Perhaps wind-ballism occurs. I did not see them liberated spontaneously after wetting and drying, as in the above *Heteropogon*. If the "eggs" (jointless) were detached as a whole, they might very well act as tumblers. Zohary (1937) mentioned a variety as synaptospermous, apparently shedding the whole "egg".

We can certainly not consider all awns as complete leaf-blades. In the case of *Aegilops* (cf. Fig. 22) nerve ribs terminate in a number of needles, also on the glumae. Are they the parallel nerves of a blade with reduced mesophyll? Also in

Mediterranean *Boissiera* five such very long, spreading "awns" arise dorsally as prolongations of dead-end nerve ribs. They may serve epizoochory, and are not hygroscopic. In this *Bromus*-alliance the spikelets form another neat analogue to the "wedge-fruits" of *Aegilops* etc. In *Enneapogon* spp. (see p.94) the lemmas of aerial spikelets have nine "awns", those of the basicarpous spikelets have none, though their glumae are long-tailed.

Tran (1965) (for later years to be cited as Tran Van Nam) gave a classification and derivation of pure form in lemmar awns, also according to tribes. Alas (naturally as a typologist) not according to either straight or geniculate-twisted, nor to convergence in function and also not comprising Bambusoideae s.l. and many-awned glumes.

We can find further transformation into awn-like structures. First in some Paniceae with weakly developed awns, connected with *Panicum*.

The infructescences of *Spinifex squarrosus* (see p. 69, 77) are disarticulated as such and tumble on long bristles. These are the nude tops of axes, bearing a fertile spikelet basally. Again, they are absent in male inflorescences. The few included caryopses were not observed as being disarticulated on the way.

The awn-like bristles between the spikelets of *Pennisetum* and *Setaria* are also not trichomes or phyllomes, but sterile axis parts, remnants of *Spinifex* conditions. In *Pennisetum* they have an anemochorous nature (soft and detached together with the spikelets). In *Setaria* their function is enigmatic, when hard and remaining on the plant after the shedding of the spikelets. In weedy species of *Setaria* with recurved hooks on the bristles there is the question of burr-like panicles, disarticulated as such, or in parts. In other species the whole may act as a shake-burr that spreads the (first arrested) grains, sometimes perhaps aiding the poor disarticulation of spikelets. This is even absent in *S. italica*, perhaps initially, perhaps bred out by cultivation. The relation with *Cenchrus*, where also complexes are set free, is illuminating. The thorns on these epizoochorous burrs are also transformed sterile branches, although usually indicated as "involucrum". Some of its species developed as endemics in Hawaii, obviously naturally dispersed.

As collateral to anemochorous telechory Scholz (1978) described, for some *Bromus* spp. from semi-arid regions, probable passive trypanocarp of deviating, many-fruited, synaptospermous (perhaps epizoochorous) spikelets. They look like *Aegilops* spikelets and are also "wedge fruits" with their tuft of bristles, as mentioned on p. 178. In one (*B. sericeus*) the tuft may assist in active burrowing as the "pappus", consisting of dry, awned, empty lemmas, can execute movements in a unique way. The flattened joints of their rachillas perform hygroscopic twists, spreading the lemmas. Again a remarkable case of convergence, if it does not just mean spreading for epizoochory. *Boissiera* is comparable.

## G. Retrospective Views

After discussion of all possible methods some retrospective remarks on strategies for dispersal and establishment may be added.



As said on p.94, Stopp (1958 b) discussed some grasses with amphicarpous atelechory, including partial basicarpy. The cleistogamous, unawned spikelets on the ground often produce much larger fruits and remain enclosed in leaf sheaths. This not only means extra protection, but also atelechory, and probably the necessity of special stimulation.

North American *Amphicarpon* almost abolished dispersal by relying on its one-seeded, geocarpous spikelets, hardly at all on its aerial ones. When some grains are dispersed together in a spikelet, different potentials for germination may be combined by differential dormancy. This has been demonstrated for *Aegilops* (see p.93), *Avena* spp. and the wild einkorn (*Triticum boeoticum*). For seed polymorphism in *Aegilops speltoides* see p. 100.

We discussed the importance of water depth for the germination of rice grasses, we compared them in this respect with forest grasses and studied devices for burrowing in more arid regions. In the latter, establishment is dependent on the right depth of implantation not only for germination, but also for rhizome formation and tillering. Their success mostly decreases with more superficial sowing, but too deep implantation can be compensated somewhat by elongation of the mesocotyl.

We have recognized the auxiliary structures around simple caryopses and in adjoining parts as components of refined, harmonious systems. They are connected not only with transport but also with presentation, fixation and germination, all under specific conditions.

One might now expect a comparative dispersal spectrum covering all the tribes discussed, and reflecting more detailed functional phylogeny in them. Some circumstances prohibit this, amongst others, some uncertainty on delimitation of units and lack of overall knowledge on dispersal methods; also frequency of diplo- and polychory and the factors outside mere transport.

Specialists might start such considerations inside genera, but there remains the circular feed-back that generic delimitations themselves may be due to factors around dispersal.

After all, we have not progressed very far from Agnes Arber's "welter of unrelated detail", but the attempts may have opened some ways to understanding. We now leave aside the artefact *Zea mays* and the exceptional *Sporobolus* (the seed escaping from the pericarp) and ask: did caryopses never manage to become independent of glumes?

This happened in such higher groups as *Agrostis* and *Eragrostis*, perhaps beginning (according to Ridley) with rolling complexes from which the very small, nude caryopses were dropped. Rabinowitz and Rapp (1979) confirmed this for *Agrostis hiemalis*: half of the seeds are shed in situ, half by rolling. Dispersal by granivorous birds, in mud on feet and by flotation, helps. A number of *Eragrostis* spp. are endemic to the Hawaiian archipelago. No burrowing? The opposite occurred rarely: fusion of caryopses with glumes, as in some *Hordeum* spp.

On dry soils birds utilize and profit from the ancestral dropping on the soil. In arid regions the inherited breaking up of the rachis can be utilized for

atelechorous burrowing by the awns. It also fits remarkably well as a pre-adaptation in the syndrome of myrmecochory (see Fig. 14). Disarticulation serves adhesive diaspores and all burrs as well, also the detachment of anemochorous parts. In diverse "needle grasses" the abscission is modified adaptively, as we saw. The silification, not originated there, served well in arid regions. In arid regions the glumes provide (as proved for cereals) protection against desiccation of caryopses.

When we return to the opening sentences it appears necessary to reflect further on the biological significance of the described diversification. In orchids it is floral, directly operative for speciation. In grasses, diversification in dispersal has an indirect conservative significance for speciation via specific arrival and establishment in niches. Direct floral speciation by isolating barriers is difficult to visualize. Although the timing of pollen shedding and receptivity with short viability of pollen may provide some specificity, the uniform anemophily of the flowers does not seem favourable to speciation. There is some indication that chaotic hybridization is further limited not only by cytological pre- or post-mating barriers, but also via harmonious dispersal, with new character combinations in their accessory fruit organs ill-fitting internally and to the vegetative requirements in the necessary biotope. This might be investigated in *Corynephorus* and was proven for 24 *Aegilops-Triticum* hybrid forms by Zohary (in Baker and Stebbins, 1965). The three dispersal mechanisms most successful in the original diploids under different climatic conditions were the only ones met with in (amphi) polyploids that became weedy in nature. All of the many other combinations in polyploids were extinguished by selection as nonsense-combinations.

One wonders why geneticists did not give more attention to such phenomena in hybrids (when fertile) between grasses with different dispersal systems: Grant (1979) stimulated this. On the other hand, in foreign regions hybrid recombinations may lead to success as weeds. Though aspects of establishment proved inseparable, we had to abstain from considering the fate of seedlings. Some literature on the subject (limited to temperate grassland) can be found in Bakker et al. (1980).

# XI. Man and His Plants in Relation to Dispersal

Many plants owe their distribution in some respect to man. They have all been indicated as anthropochores, in a wide sense. This is too wide a sense, as man is not the direct agent of dispersal for all of them, often only producing the right substrate. The unfortunate use of "anthropochores" for "anthropophytes" causes strange sentences like: "we found a high percentage of anemochores in anthropochores".

Seen from the historical, floristic-regional standpoint, new arrivals are indicated as adventive plants or neophytes. The latter term is, however, often reserved for entirely naturalized species (perhaps arrived naturally) that are at present independent of human activity.

The grass *Spartina townsendi* is a neophyte in a double sense, being a new, amphidiploid species which conquered new territories in tidal mud in Western Europe by natural means.

Naegeli and Thellung (1905), give a classification of weeds in genetic groups, designating all plants bound to man and his actions as anthropophytes. The term "anthropophiles", used as a collective noun, should be avoided because of nomenclatural confusion with pollination classes. Under the (older) name "apophytes", the above authors lift out a group composed of those native plants that switch in mass to places influenced by human habitation; the remainder of the weeds they consider to be the true anthropochores. The so-called ruderal plants consist of native and introduced plants bound to special habitats, often also created by human activity. They may, therefore, be classified vaguely under anthropogene vegetation or as anthropophytes. Early man selected a number of cultivated plants from ruderals growing spontaneously near his dwellings, but these are as a group not necessarily anthropochores. The concept of weeds as small plants is not generally valid, as *Prunus serotina* shows for Europe. The inhabitants of tropical secondary forests may be indicated as woody weeds, as introduced *Salix* is in New Zealand. We saw (cf. *Prosopis* and *Acacia*) that natural woody successors in more or less artificially maintained pasture land are also considered as such in cattle ranges.

The number of further terms and classifications is great and of so little importance for our limited purpose that I refer to only one recent review of anthropophytes, viz. Schroeder (1969).

In recent years sociological, floristic classification has been tried (Tüxen, 1966).

The term "anthropochores" could also be applied to plants introduced intentionally, but not connected with human activity in their further dispersal

and distribution because natural dispersers took over. Instances are bird-dispersed *Lantana camara* in Java and *Prunus serotina* in Europe, both discussed before, and also the introduced anemochores and other escapees from gardens.

We may also omit all cultivated plants (as long as they do not spread spontaneously), since their dispersal seems to lie outside our chosen field; on the other hand, plant geographers have to consider them as anthropochores outside their natural regions. Historical studies in this field we have to leave aside, but these, on their side, have to reckon with dispersal ecology, among other factors, with the capacity of parts to survive travel in the company of man and to travel spontaneously. Even a short discussion of the puzzles concerning the origin and dispersal of *Nicotiana*, *Zea*, *Lagenaria*, *Cucurbita*, *Ipomoea*, *Gossypium* etc. would be out of place here.

The changes effected during long cultivation, and the reconstruction of the genetic makeup of the original diaspores, also belong to the biological side of such studies.

Earlier, we saw that the functions of dormancy and dispersal were often discriminated against in agriculture. Certain natural properties of diaspores, such as the disintegration of cereal spikes, the synaptospermy of *Beta*, the dissemination of seeds in flax and poppies, the presence of seeds in oranges and the penetrating odour of bat-fruits (in wild-type *Mangifera* species), were simply a nuisance to man. The same holds for the natural dispersers, which were mentally degraded to the rank of robbers (e.g. bats in the case of dates). Cultivated *Zea* seems an "impossible" plant in its domestication, devoid of all natural dispersal ability. Knowledge of natural pollinators and dispersers cannot be dispensed with in studies concerning the geographical origin of cultivated plants. Examples are *Musa Fehi* and *Artocarpus incisa* (van der Pijl, 1957) in Hawaii.

Our main interest, however, lies in our involuntary companions, the weeds, or more generally and neutrally described, the fast colonizers of new, disturbed territories.

The effect exerted by man lies firstly in the field of ecesis, in the new open habitats he creates. The opening of arable land in a forested region like Java found few natural weed-candidates, since most plants were shadow-loving, with the exception of some natural pioneers. The country was overrun by invaders, now numbering 300 species. An early list of these contains 65 Americans, 25 Europeans, 16 Asians, 5 Africans and 1 Australian, as well as many of uncertain origin. Ridley gave a comparable list for Singapore. Mulligan (in Baker and Stebbins, 1965) reports on the mainly European, weedy invaders in Canada, which are dominant over much of the settled area. He stresses their wide range of tolerance, their polyploidy (46% of the 150 most common weeds) and the ability of their seeds to germinate at any time when favourable circumstances are present.

In sunny California, native opportunity was left open, but there was a large influx from the eastern Mediterranean region. Stebbins (in Baker and Stebbins, 1965) estimates that the hundreds of weeds in the agricultural regions there



(which have been established since 1750), comprise about 40 apophytes with colonizing tendencies, partly composites. The Levantines had long before been adapted as weeds.

In Europe, colonization by "anthropochores" is so old that an evaluation of individual cases is difficult and can often be based only on bonds with disturbed soil. Godwin, in his "*History of the British Flora*" (1956) has shown that much of the weed flora was present in glacial times before the arrival of neolithic man, though early flowering summer annuals seem to be postglacial.

New Zealand was a paradise for invaders, which have transformed the vegetation within a century. In 1949 the number of aliens, naturalized since 1799, was about one thousand.

The other side of the picture is presented by the plants, in their aggressiveness, expressed also by a high ratio of photosynthates used for reproduction vs. growth and respiration. In order to be successful, they must, of course, possess means of abundant seed production and fast dispersal, but this is not the whole truth. The list of the most successful weeds of our planet contains not only those "focussing" on dispersal mechanisms; their genetic makeup must also be suited to the special requirements. This more modern viewpoint was the topic of a symposium, already referred to (Baker and Stebbins, 1965). Stebbins postulated here that there exists no relationship between the size of a native genus and its chance of producing a weed, so that special, preadaptive properties seem necessary. Baker discussed some large genera of the Composites that possess seeds with a pappus (*Tridax*, *Eupatorium*, *Ageratum*), finding each with but a single or a few species, especially annuals, that act as weeds. Ehrendorfer discussed Dipsacaceae in connection with fruit diversity, pollination and cytotaxonomy.

We must here pass over the much-discussed general plasticity, the advantage of certain breeding systems (selfers relatively preferred, as well as unspecialized pollination), of a certain ploidy-level (a rather controversial point), of possible adaptation to day-length, of the length of the life cycle and of high germination potential. Sometimes success as a weed was delayed until genetic readjustment had taken place, possibly by introgression with natives. Interesting points were raised by Baker (in Valentine, 1972). In 1974 he presented many references on how weeds evolved. Mulligan and Findlay (1970) demonstrated the preponderance of autogamy.

The relation between a high ploidy-level and aggressivity has also been studied by Pignatti (in Tüxen, 1966). The level proved to be equal in pioneers in natural and anthropogenous vegetations, and a high level is assumed to have been effective in reconquest after glaciation.

This limitation notwithstanding, we cannot forego paying some more attention here to our viewpoint, the transport factor – which after all is also part of the plant's genetic constitution. It is not accidental that those families mentioned on p.98 as having most refinements for dispersal, are also the major producers of weeds. Zohary Jr. discussed in the symposium the importance of dispersal types in a group of "wheats" which became weedy (see p. 182).

Dispersal plasticity of weeds has been mentioned as an important factor in the sections on heterocarpy and polychory. The many remarks on the harmony between habitat and dispersal need not be repeated and listed here in relation to weeds. The connection with man and agriculture may also have brought about changes in them, sometimes converting a weed into a crop plant (oats, beets).

In the case of *Avena* the loss of detachment of diaspores (present in natural forms) seems to have automatically promoted them from weeds to crop plants between other cereals.

In Müller (1955), we find data on *Sonchus* species, originally purely anemochorous but gradually shifting to anthropochory by adhesion, during long contact with agriculture. The special group of weeds growing among crop plants (e.g. in fields of pulses and flax), had to conform to these in many respects, as one can easily learn from a comparison with the wild forms. The general habit, the period and periodicity of germination and maturation, and the size of the seeds are curiously similar, in fact, almost identical. Vavilov applied here the term "mimicry", already so often misused for a likeness without ecological function. In this case it is due to human interference with weeding, harvesting and seed purification.

A third aspect in the development of weeds (after genetic adaptability and dispersal plasticity), not emphasized in the symposium mentioned, must be the synecological one of their escape from natural competitors and antagonists. In this respect the term "fugitive species" would be suitable, though it is often applied to those in unstable margins.

The artificial escape from competitors and limiting factors of pollination and ecesis enabled species with very limited area to deploy their dispersal potential. This was demonstrated by Marie-Victorin (1938). Such "relict Compositae" as *Solidago multiradiata* (in contradiction to what was stated by Croizat on p. 4), after transplantation to Montreal, underwent explosion into a weed. The means of dispersal had simply been suppressed before. Sheldon and Burrows (1973) discussed cases of seeming inefficiency in dispersal.

Many adventive plants owe their new distribution to the trade in grains and wool. The fleece of sheep can carry burrs, which are then still farther transported with the wool. The history of the migration of *Xanthium* into South America and Australia is tied up with the migration of sheep. *Medicago denticulata*, after its introduction into Australia, became, as "burr-medic" obnoxious to the wool trade. The migration of weeds in crops is, likewise, not immediately anthropochorous or even epizoochorous. The main factor, overriding the transport of the products by man, is that they must be suited to the conditions for the crop; their diaspores also must bear a certain likeness to those of the crop. All alien plants indirectly connected with human activity for their distribution and/or dispersal were indicated in Finland (by Linkola) as hemerochores (*hemero* = tamed or civilized).

The anthropochores *sensu stricto* cling to man and his gear as just a case of special epizoochory, but include the train of his crops. A thorough discussion would reflect man's ecology (the "ecology" of activists etc.) more than that of

plants. Falinski (1972) considered the group as distinct because of bonds with activities peculiar to man. One illustration is presented: Apparently non-epizoochorous diaspores are attracted electrically to clothing with static, due to the rubbing of artificial fibres in tissues.

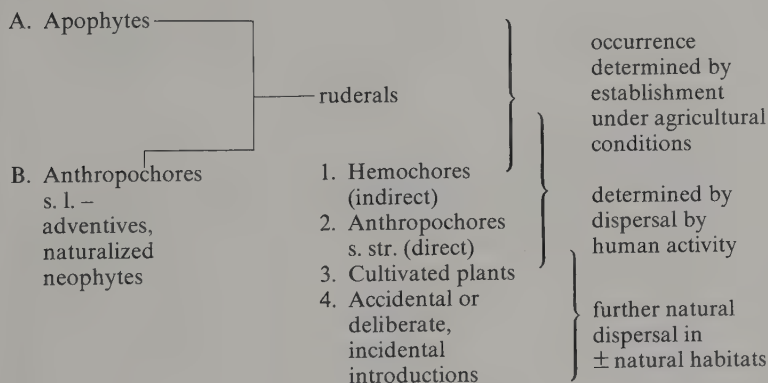
Some authors, especially Eastern Europeans, produced classifications according to actual ways of human transport: in grains, in wood, by train and airplane or on cattle. This involves few new biological principles, and readers interested in an enumeration of cases and historical details, are, therefore, invited to consult Ridley or the works dealing with alien elements in each national flora. The book by Thellung (1930) also is a rich source of information on weeds.

Endozoochorous dispersal by man may have been important in archaic civilizations. Human feces were avoided as dung by American Indians because of field-infestation with *Opuntia*. Tomato seeds also survive in them.

Californian Indian tribes collected all feces for a "second harvest", of picked-out cactus seeds (of *Lemairocereus*) to be ground into flour.

Rick and Bowman (1961) mentioned American Indians as treating seeds before planting by eating them first.

The intricate analysis of anthropophytes or synanthropes can be summarized in the following scheme:



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